Diversity and assemblage composition of terrestrial herbaceous plants in tropical forest and agroforest

---

Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde

(Dr. sc. nat.)

vorgelegt der

Mathematisch-naturwissenschaftlichen Fakultät

der

Universität Zürich

von

Daniele Cicuzza

aus

Italien

Promotionskomitee

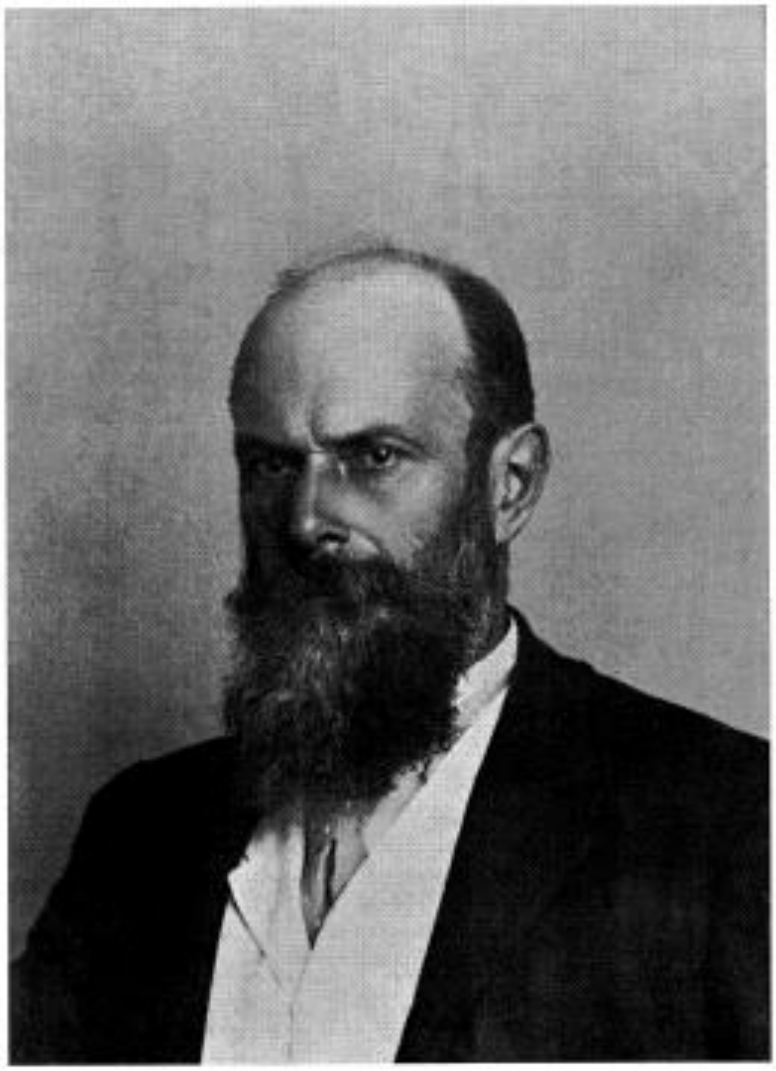
PD Dr. Michael Kessler (Vorsitz)

Prof. Dr. H. Peter Linder

Prof. Dr. Florian Schiestl

Zürich, 2010

Table of contents



I dedicate my Doctor of Philosophy Thesis to the Italian botanist Odoardo Beccari.

"Ma la foresta del Borneo é così multiforme nelle varie ore del giorno e a seconda della stagione e del tempo, che nessuna descrizione riuscirà mai a farne acquistare un'adeguata idea a chi non vi abbia vissuto. Infiniti e variati sono gli aspetti sotto i quali si presenta, come i tesori che nasconde. Le sue bellezze sono inesauribili. Nella foresta l'uomo si sente veramente libero; quanto più la studia e tanto più si accorge che non riesce a conoscerla. Il suo mistero, sacro alla scienza, tanto appaga lo spirito del credente, quanto quello del filosofo indagatore"

Odoardo Beccari

INTRODUCTION

Deforestation is the major process of tropical forest destruction causing the lost of tropical biodiversity. This process determines the disjunction of forest patches, from the native forest. The fragmentation, maximizing the effect of forest edge, has a negative impact on the native population of plants and animals (Sodhi *et al.* 2010). The forest margin is defined as the areas which include the forest edge and the agricultural land use system, which usually surround the forest (Tscharntke *et al.* 2007). Although the establishment of national parks, preservation of natural connections between reserves in order to facilitate population exchange, still remains the most important strategy for conservation, the stability and conservation of forest margin has been recognized as a critical factor for preservation of tropical forest (Müller & Zeller 2002). Deforestation is partly represented by conversion in plantation of cacao and coffee trees (Bhagwat *et al.* 2008). Due to their shade ecology, seedling of cacao and coffee trees grown under the shade of higher trees, which are often represented by natural forest trees. This specific crops production, called agroforestry system, represents the most forest like landscape (Bhagwat *et al.* 2008). It has been addressed as a strategic environment for tropical diversity conservation, outside national parks (Bhagwat *et al.* 2008). In Indonesia, and in Sulawesi in particular, process of tropical forest conversion to cacao plantation has represented, in the last decades, an important change in the regional landscape (Erasmi *et al.* 2004). In this context an interdisciplinary project, Stability of Rainforest Margin in Indonesia (STORMA), was established from the University of Göttingen (Germany) in collaboration with the following Indonesian institutions: Bogor Agricultural University (Bogor, Java), Tadulako University (Palu, Sulawesi), and the Indonesian Institute of Science (LIPI). Field research is conducted inside and around the Lore Lindu National Park located on the island of Sulawesi, recognized as a hotspot of biodiversity in the Wallaceae area (Myers *et al.* 2000). The agroforestry system, surrounding the national park, represented largely by cacao plantations is studied in its process of agricultural intensification.

The study gives to us the possibility to understand in which degree this ecosystem play a role in the biodiversity conservation. Moreover the project studies the socio-economy trade-off with a better agroforestry management, and the different possible future scenario testing with integrating land-use models. The present PhD thesis is included in the frame work of the STORMA project.

Herbaceous diversity in tropical forest

Tropical forests are by far the richest biodiversity terrestrial biomes and trees are an important part of these biomes. They characterize the forest structure, determining the different forest layers and provide a support for climbers and epiphytes. Most of the studies conducted in tropical forest have taken in consideration the trees diversity while tropical forest herbs were often ignored or seldom collected. With the developing of more accurate collecting technique, like permanent plot sampling, not only the whole woody components but also the herbaceous species were collected and identified. These results give to us a much clearer view of tropical plants diversity, distribution, ecology and biological interactions. The herbaceous components of tropical forest are the terrestrial and epiphytic angiosperm, pteridophytes and lycophytes. Gentry (1982), highlighted the importance of forest tropical herb diversity in the overall tropical species richness. Since Gentry only very few studies have been conducted to better understand herb communities in tropical biomes. For this reason our knowledge on herb richness, composition, distribution, ecology and response to the environmental factors still needs an intense effort and at the same time our actual knowledge is not equal among the three tropical biomes (America, Africa, and Asia). Many of the tropical families have a pantropical distribution (Heywood *et al.* 2007) with an unequal number of species along the three equatorial areas. For example Zingiberaceae (gingers family), although they are a pantropical family, the center of diversity is shifted in South East Asia (Larsen *et al.* 1998). This discrepancy in species richness is due to the geological history of the area, family evolution, rate of speciation and extinction and also dispersal strategy. Ferns and lycophytes have a different reproduction strategy, in comparison

with angiosperms, and their easier dispersal strategy, determine that ferns and lycophytes tend to have a wider distribution and families tend to be present homogeneously within the three tropical terrestrial biomes (Moran 2008). Herb species composition has been assessed using a variety of methods including plot surveys (Potts *et al.* 2002), transects (Hanna & Kalle, 1994, Costa *et al.*, 2002) complete inventory of a 1 ha. forest (Poulsen 1996). The study of terrestrial herb diversity, richness and distribution has shown how they are correlated with climate, soil characteristics and orography. Studies in tropical forests (Poulsen *et al.*, 2006) found how small differences in soil characteristics can determine the changes in community species composition. Other important elements which can play a role in herb distribution and richness are exposure (Costa, 2006), elevation (Kluge *et al.* 2006) and seasonal change in landscape (Tuomisto *et al.*, 2003). A more comprehensive study on flowering plants (including trees, shrubs and climbers), it has been shown at global level that a combination of high annual energy input with constant water supply and extraordinary topographic complexity, are able to accurately predict the areas of global center of plant diversity (Kreft & Jetz, 2007).

Herbaceous diversity in Agroforestry Systems

Indonesia has experienced an increase of severe deforestation over the last decades; Sulawesi in particular has seen a constant increase of conversion from tropical forest to cacao plantations (Erasmi *et al.* 2004). Worldwide the agroforestry system is mainly represented by cacao and coffee plantations (Bhagwat *et al.* 2008). The agroforestry system is characterized by crops, where seedlings develop under the shade of older trees, represented principally by natural forest, or planted trees. The presence of these different layer of trees determine that the agroforestry system resemble a natural wood habitat. The process of conversion from natural forest in agroforestry system, has the same pattern of change in the, cacao and coffee plantations. Our project aim was concentrated on cacao plantation; therefore henceforth we consider only the cacao agroforestry system. The agriculture intensification process is characterized by three important structural categories: (1) rustic cacao, (2) planted shade and (3) technified cacao (Rice

& Greenberg 2000). Rustic cacao is where the crops are planted beneath thinned primary or old secondary forest. Planted shade agroforesty ranges from the traditional polyculture through commercial, to a specialized and single shade species. The final category, technified cacao is when there is no shade component above the cacao (Rice & Greenberg 2000, Steffan-Dewenter *et al.* 2007, Perfecto & Snelling 1995, Moguel & Toledo 1999). To some degree this system provides important habitats for birds (Sodhi *et al.* 2005, Abrahamczyk *at al.* 2008, Clough *et al.* 2009), amphibians and reptiles (Wanger *et al.* 2009), bats (Faria *et al.* 2006), bryophytes (Ariyanti *et al.* 2008), and trees (Sambuichi *et al.* 2007, Zapfack *et al.* 2002, Sonwa *et al.* 2007). The animal and plant groups react differently to habitat factors and are therefore represented separately in agroforestry systems (Steffan-Dewenter *et al.* 2007, Kessler *et al.* 2009). The process of cacao intensification dramatically reduces the tree species composition (Rice & Greenberg 2000, Kessler *et al.* 2005). At the same time the increase of the land-use change determine the increase of species abundance of determinates groups. For instance the changes in canopy structure modify light intensity and air humidity, which result in a cascade effect that changes the suitable environment for animal groups such as ants, (Kaspari *et al.* 2000, Philpott & Armbrecht 2006), and epiphytes (Andersson & Gradstein 2005). The increase of light intensity in the planted shade-tree category resulted in a greater herbaceous species number, primarily due to the presence of weedy species. (Zapfack *et al.* 2002). The agroforestry system may help to maintain a certain portion of diversity, but not of all taxonomic groups. However their single observation in the agroforestry system does not guarantee ecosystem functionality over a long period.

Ground-living herbaceous plants have so far largely been ignored in biodiversity assessments of agroforestry systems even though herbs provide food or structural habitats for a wide range of animals (Höhn *et al.* 2009, Bos *et al.* 2007, Wanger *et al.* 2009). In these systems herbs have been studied in Brazil (Faria *et al.* 2007), Cameroon (Bobo *et al.* 2006), and Indonesia (Ramadhanil *et al.* 2008, Steffan-Dewenter *et al.* 2007). The composition of herbaceous species in agroforestry systems are influenced by numerous factors such as the distance from natural forest (Perfecto & Vandermeer 2008), management regimes (Bos *et al.* 2007, Ariyanti *et al.* 2008, Philpott *et al.* 2008), and tree structure and composition (Perfecto &

Vandermeer 2008). The results commonly show that agroforestry systems harbour a higher diversity of terrestrial herbs than in natural forests. Considering the ecology of these species many of these herbs are widespread, weedy, and often alien species (Backer 1973).

This thesis deals with the study of terrestrial herbaceous community composition in the tropical forests of the Lore Lindu National Park in Central Sulawesi (Indonesia) and the surrounding cacao plantations in two different valleys. Herb diversity in the tropical forest was first studied extensively with more than 400 plots (5x5m) than along the altitudinal gradient from 250 to 2450m a.s.l., with an addition of 204 plots (5x5m), in order to have a clear representation of environmental variety present in the Sulawesi tropical forests. The studied on terrestrial herbaceous species was also conducted outside the Sulawesi Island as Borneo, Bali, Malaysia, La Reunion, Congo, Uganda, Bolivia, Costa Rica and Mexico. These studies, at different scale of analysis, but using the same methodology, give to us the possibility to have a proper understanding of herbaceous community composition and their relation with the environmental factors at local scale, along the altitudinal gradient and at the intercontinental scale.
In the cacao agroforestry system, surrounding the Lore Lindu National Park, I studied the herbaceous diversity and their changes over a two year period. In the two valleys 43 cacao plantations were rented by the local farmers and within each plantation I established two plots for a total of 86 plots. In addition the diversity in composition changes was studied by the application of different agricultural management techniques. With this study I want to know the herbaceous species composition in the cacao agroforesty system, how the conversion influence the species composition and in particular which forest herbaceous species are influenced, moreover does different management determine the species composition and a simplification of it with weedy and pantropical species.

In **chapter one** I focus on terrestrial herbs of the cacao plantations in two valleys of central Sulawesi. The plantations ranged from near the tropical forest margin through to the complexity of the tropical matrix landscape. Plantations were distributed across two valleys (22

in Kulawi and 21 in Palolo) including most of the different landscape heterogeneity (shade intensity, distance from the forest margin and elevation). In each plantation I established two plots of 40 m x 40 m plots, within each plot I set apart a 5 m x 5 m plot for our herb survey, for a total of 86 plots.

My aims are to determine the taxonomic composition and diversity of herb flora in cacao plantations and to highlight which environmental factors and management practices influences the terrestrial herb diversity. More closely, will be distinguished the contribution of forest species, weedy and pantropical species. Furthermore I want to highlight the role that a cacao agroforestry system plays in the conservation of native herbaceous forest species.

Management of cacao plantations can change the composition and abundance of herbaceous species. Fertilization not only increases the cacao yield but increase the herbaceous layer which compels the farmers to weed the herb understory. Moreover fertilization increases the herbaceous biomass production. On the other hand we do not know if fast growing herbs are facilitating from the fertilization and detriment to other species. The frequency of weeding can shift the composition and abundance of herbs species, increasing the weeds. In **Chapter two** I conducted the high/low fertilizer application frequency and high/low weeding frequency managements. In this way I analyzed whether species richness, abundance, biomass and composition of terrestrial herb assemblages changed over time with respect to these management practices. I also wanted to determine whether a determinate set of species are correlate with particular management practices. Finally I want to establish whether there was a relationship between the native and weedy species and the management regimes.

Sulawesi is one of the most under-collected islands in both Indonesia and in South East Asia (Cannon, 2007). The knowledge of biodiversity within this island is important especially in the nowadays ongoing process of deforestation. In **chapter three** I study the alpha diversity of terrestrial herbs and their distribution in two study areas, Pono and Bariri, at the respective elevation of 1000 and 1400m a.s.l. To study the herb diversity I established 200 plots (5x5 m^2) in each of the two study areas, for a total of ca. 0.7 km^2. Each site had a specific design in order to include the orographic and environmental diversity. To overcome the difficulties faced with

respect to species identification I analyzed the whole flowering plant flora at the family level. In contrast pteridophytes were identified to the species level.

In this study I addressed the following questions: (i) how many terrestrial herbs species are present at the two tropical mountain forest sites in Lore Lindu National Park, (ii) how different is the species composition between these two areas, and (iii) how is characterizes the terrestrial pteridophytes assemblage in Bariri and Pono?

Elevational gradients offer an outstanding opportunity to study and understand patterns of biotic diversity as they represent a reproducible environmental gradient that can be used at a global scale (Lomolino 2001, McCain 2009). Along the altitudinal gradient biodiversity tend to increase up to a certain elevation, depending to the site take in consideration, with a subsequent decrease, the causes of this 'hump-shaped' curve, presented in several studies (McCain, 2007) are largely unknown, but are often taxon-specific and depend on the spatial as well as the geographical location of the gradients (Rahbek 2005). In **chapter four** I present a study conducted from the lowlands to the highest mountain peak in central Sulawesi, spanning an altitudinal range from 250 to 2450 m a.s.l. with 22 transects of 12 plots each of 5 x 5 m^2, separated by intervals of 35 m. The aim is to document the patterns of species richness of terrestrial forest herbs along an elevational gradient in central Sulawesi and to identify possible correlations with environmental factors. Specifically, I asked the following questions: (i) how does terrestrial herb diversity change along the elevational gradient? (ii) Do different taxonomic groups show similar patterns? (iii) Which are the environmental and geographic factors that correlate best with herb diversity?

Many studies on terrestrial tropical herbs have been conducted at a regional scale and with different sampling techniques. Their results have shown that at this scale such factors as soil and orography strongly influence the herb composition and distribution (Costa *et al.* 2006 Poulsen *et al.* 2006, Tuomisto *et al.* 2003). Only recently the worldwide diversity has been studied correlating with environmental factors. In flowering plants (including trees, shrubs and climbers), has been shown at global level that a combination of high annual energy input with constant water supply and extraordinary topographic complexity, are able to accurately predict the areas of global center of plant diversity (Kreft & Jetz, 2007). For terrestrial herbs due to the

methodological differences conducted in these studies it has not been possible to compare herb diversity over a broader region, such as across the three continents, America Africa and Asia. In **chapter five** I conduct a comparatively study of terrestrial herb diversity in tropical forests across the three continents, in the following areas: Sulawesi, Borneo, Bali, Malaysia, La Reunion, Congo, Uganda, Bolivia, Costa Rica and Mexico. I conducted 86 transects of 12 plots each of 5 x 5 m^2, separated by intervals of 35 m Specifically, herb diversity, analyzed at the family level, with presence/absence data from America, Africa and South East Asia was compared with elevation, temperature, precipitation and area, The aim of this chapter is to underline the pattern of diversity of terrestrial tropical herbs forest in the three continents and relate these to elevation and climatic data.

STORMA Website: http://www.uni-goettingen.de/de/40515.html

REFERENCES

Abrahamczyk, S., M. Kessler, D. Putra, M. Waltert, & T. Tscharntke (2008) The value of differently managed cacao plantations for forest birds conservation in Sulawesi, Indonesia. *Bird Conservation International* 18: 349-362.

Anderson, M.S. & S.R. Gradstein (2005) Impact of management intensity on non-vascular epiphytic diversity in cacao plantations in western Ecuador. *Biodiversity and conservation* 14: 1101-1120.

Ariyanti, N.S., M. Bos, K. Kartawinata, S.S. Tjitrosoedirdjo, E. Guhardja. & S.R. Gradstein. (2008) Bryopytes in tree trunks in natural forests, selectively logged forests and cacao agroforests in Central Sulawesi, Indonesia. *Biol. Conserv*. 141: 2516-2527.

Backer, C.A. (1973) Atlas of 220 weeds of sugar cane fields in Java. In Backer, C. A. (Ed.). Indonesian Sugar Experiment Station Pasuruan, Indonesia.

Bhagwat, S.A., K.J. Willis, H.J.B. Birks & R.J. Whittaker (2008) Agroforesty: a refuge for tropical biodiversity? *Trend in Ecology and Evolution* 261-267.

Bobo K.S., M. Waltert, N.M. Sainge, J. Njokagbor, H. Fermon, & M. Mühlenberg. (2006) From forest to farmland: species richness patterns of trees and understory plants along a gradient of forest conversion in Southwestern Cameroon. *Biodivers. Conserv*. 15: 4097-4117.

Bos, M.M., P. Höhn, S. Saleh, B. Büche, D. Buchori, I.S. Dewenter, & T. Tscharntke. (2007) Insect diversity responses to forest conversion and agroforestry management. In Tscharntke T., C. Leuschner, M. Zeller, E. Guhardja, A. Bidin. (Eds.). The stability of tropical rainforest margins, linking ecological, economic and social constraints of land use and conservation, pp. 279-296. Springer, Berlin.

Cannon, C., H. Summers M., J.R. Harting, & P.J.A. Kessler (2007) Developing conservation priorities based on forest type, condition, and threats in a poor known ecoregion: Sulawesi, Indonesia. *Biotropica* 39: 747-759.

Costa, F.R.C. (2006) Mesoscale gradients of herb richness and abundance in central amazonia1. *Biotropica*, 38: 711-717

Costa, F.R.C., C. Senna, & E.M Nakkazono (2002) Effects of selective logging on populations of two tropical understory herbs in an amazonian forest1. *Biotropica*, 34: 289-296

Clough, Y., D. Dwi Putra, R. Pitopang, & T. Tscharntke (2009) Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry. *Biol. Conserv.* 142: 1032-1041.

Davis. A.J., J.D. Holloway, H. Huijbregts, J. Krikker, A.H. Kirk-Spriggs, & S.L. Sutton (2001) Dung beetles as indicator of changes in the forest of northern Borneo. J*ournal of Applied Ecology,* 38: 593-616.

Erasmi, S., A. Twele, M. Ardiansyah, A. Malik, & S. M. Kappas. 2004. Mapping deforestation and land cover conversion at the rainforest margin in Central Sulawesi, Indonesia. *EARSeL e Prooceedings.* 3: 388-397.

Faria, D., R.R. Laps, J. Baumgarten, & M. Cetra (2006) Bat and birds assemblages from forests and shade cacao plantations in two contrasting landscape in the Atlantic Forest of southern Bahia, Brazil. *Biodivers. Conserv.* 15: 587-612.

Faria, D., M.L.B. Paciencia, M. Dixo, R.R. Laps, & J. Baumgarten (2007) Ferns, frogs, lizards, birds and bats in forest fragments and shade cacao plantations in two contrasting landscapes in the Atlantic Forest, Brazil. *Biodivers. Conserv.* 16: 2335-2357.

Gentry, A.H. (1982) Neotropical Floristic Diversity: Phytogeographical Connections Between Central and South America, Pleistocene Climatic Fluctuations, or an Accident of the Andean Orogeny? *Annals of the Missouri Botanical Garden*, 69: 557-593.

Hanna, T. & Kalle, R. (1994) Distribution of pteridophyta and melastomataceae along an edaphic gradient in an amazonian rain forest. *Journal of Vegetation Science*, 5: 25-34

Heywood, V.H., R.K. Brummitt, A. Culham, & O. Seberg. (2007) Flowering plant families of the world. Firefly Books (Eds.) U.S.A.

Höhn, P., I.S. Dewenter, B. Damayanti, & T. Tscharntke. 2009. Spatiotemporal density patterns of the pest predator Rhynchium haemorrhoidale (F.) along a land-use gradient in cacao agroforestry systems. *Agroforest Syst.* 76: 163-171.

Kaspari, M., & M. D. Weiser. (2000) Ant activity along moisture gradients in a neotropical forest . *Biotropica,* 32: 703–711.

Kessler, M., P. Kessler, S. Gradstein, B. Kerstin, M. Schmull, & R. Pitopang. (2005) Tree diversity in primary forest and different land use systems in Central Sulawesi, Indonesia. *Biodiv. Conserv.* 14: 547-560.

Kessler, M. (2009) The impact of population processes on patterns of species richness: Lessons from elevational gradients. *Basic and Applied Ecology*, 10: 295-299.

Kluge, J., M. Kessler, & R.R. Dunn, (2006) What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecology and Biogeography,* 15: 358-371.

Kreft, H. & Jetz, W. (2007) Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences of the United States of America,* 104: 5925-5930

Larsen, K., J.M. Lock, H. Maas, & P.J.M. Maas, (1998) Zingiberaceae. In K. Kubitski (Eds.) The families and genera of vascular plants. pp:474-495. springer, Berlin.

Lomolino M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecol Biogeogr.* 10: 3-13

McCain, C.M. (2007) Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography,* 16: 1-13.

McCain, C.M. (2009) Global analysis of bird elevational diversity. *Global Ecology and Biogeography,* 18: 346-360.

Moguel, P., & Toledo V.M. (1999) Biodiversity conservation in traditional coffee systems of Mexico. *Conserv. Biol.* 13: 11-21.

Moran, C.R. (2008) Diversity, biogeography and floristics. In Ranker, T.A. & Haufler C.H. (Eds.) Biology and Evolution of ferns and lycophytes. pp: 367-394. Cambridge, UK.

Muller, D., Zeller, M. (2002) Land use dynamics in the central highlands of Vietnam: a spatial model combining village survey data with satellite imagery interpretation
Agricultural Economics. 27: 333-354.

Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, Gustavo, & J. Kent (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

Perfecto, I., & R. Snelling. (1995) Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. *Ecol. Appl.* 5: 1084-1097.

Perfecto, I., & J. Vandermeer. (2008) Biodiversity conservation in Tropical Agroecosystems, a new conservation paradigm. *Ann. NY. Acad. Sci*. 1134: 173-200.

Philpott, S.M., & I. Armbrecht (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecol. Entomol.* 31: 369-377.

Philpott, M.S., P. Bichier, R.A. Rice & R. Greenberg. (2008) Biodiversity conservation, yield, and alternative products in coffee agroecosystems in Sumatra, Indonesia. *Biodiv. Conserv.* 17: 1805-1820.

Potts, M.D., P.S. Ashton, L.S. Kaufman, & J.B. Plotkin. (2002) Habitat patterns in tropical rain forests: a comparison of 105 plots in Northwest Borneo. *Ecology,* 83: 2782-2797.

Poulsen, A.D. (1996) Species richness and density of ground herbs within a plot of lowland rainforest in north-west borneo. *Journal of Tropical Ecology*, 12: 177-190.

Poulsen, A.D., Tuomisto, H. & H. Balslev. (2006) Edaphic and floristic variation within a 1-ha plot of lowland amazonian rain forest1. *Biotropica*, 38: 468-478.

Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography,* 18: 200-205.

Ramadhanil, P., S.S. Tjitrosoedirdjo, & D. Setiadi. (2008) Structure and composition af understory plant assemblages of six land use types in the Lore Lindu National Park, Central Sulawesi, Indonesia. *Bangl. J. Plant Taxon,* 15: 1-12.

Rice, R.A., & R. Greenberg. (2000) Cacao cultivation and the conservation of biological diversity. *Ambio*, 29: 167-173.

Sambuichi, R.H.R., & M. Haridasan. (2007) Recovery of species richness and conservation of native Atlantic forest trees in the cacao plantations of southern Bahia in Brazil. *Biodivers. Conserv.* 16: 3681-3701.

Schulze, C.H., M. Waltert, P.J.A. Kessler, R. Pitopang, D. Veddeler, M. Mühlenberg, S.R. Gradstein, C. Leuschner, I. Steffan-Dewenter, & T. Tscharntke. (2004) Biodiversity indicator groups of tropical land-use systems: comparing plants, birds and insects. *Ecol.Appl.* 14: 1321-1333.

Sodhi, N.S., L.P. Koh, D.M. Prawiradilaga, Darjono, I. Tinulele, D.D. Putra, & T.H.T. Tan. (2005) Land use and conservation value for forest birds in central Sulawesi (Indonesia). *Biol. Conserv.* 122: 547-558.

Sodhi, N.S., L.P. Koh, R. Clements, T.C. Wanger, J.K. Hill, K.C. Hamer, Y. Clough, T. Tscharntke, M.R.C. Posa, & T.M. Lee (2010) Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biological Conservation* 143: 2375-2384.

Sonwa, D.J., B.A. Nkongmeneck, S.F. Weise, M. Tchatat, A.A. Adesina, & M.J.J. Janssens. (2007) Diversity of plants in cocoa agroforests in the humid forest zone of Southern Cameroon. *Biodivers. Conserv.* 16: 2385-2400.

Steffan-Dewenter, I., M. Kessler, J. Barkmann, M.M. Bos, D. Buchori, S. Erasmi, H. Faust, G. Gerold, K. Glenk, R.S. Gradstein, E. Guhardja, M. Harteveld, D. Hertel, P. Höhn, M. Kappas, S. Köhler, C. Leuschner, M. Maertens, R. Marggraf, S. Migge-Kleian, J. Mogea, R. Pitopang, M. Schafer, S. Schwarze, S.G. Sporn, A. Steingrebe, S.S. Tjitrosoedirdjo, S. Tjitrosoedirdjo, A. Twele, R. Weber, L. Woltmann, M. Zeller, & T. Tscharntke. (2007) Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proc. Natl. Acad. Sci.* USA 12: 4973-4978.

Schultze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D., Muehlenberg. M., Gradstein, S.R., Leuschner, C., Stefan-dewenter, I. & Tscharntke, T. (2004) Biodiversity indicator groups of tropical land-use system: comparing plant birds, and insects. *Ecological applications,* 14: 1321-1333.

Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003) Dispersal, environment, and floristic variation of western amazonian forests. *Science*, 299: 241-244,

Wanger, T.C., A. Saro, D.T. Iskandar, B.W. Brook, N.S. Sodhi, Y. Clough, & T. Tscharntke. (2009) Conservation value of cacao agroforestry for amphibians and reptiles in Southeast Asia: combining correlative models with follow-up field experiments. *J. Appl. Ecol.* 46: 823-832.

Zapfack, L., S. Engwald, B. Sonke, G. Achoundong, & B. Madong. (2002) The impact of land conversion on plant biodiversity in the forest zone of Cameroon. *Biodivers. Conserv.* 11: 2047-2061.

Conservation value of cacao agroforestry systems for terrestrial herbaceous species in Central Sulawesi, Indonesia

Daniele Cicuzza[1], Michael Kessler[1], Yann Clough[2], Ramadhanil Pitopang[3], Daniela Leitner[4] and Sri S. Tjitrosoedirdjo[5].

[1]*Institute of Systematic Botany, University of Zurich, Switzerland.*
[2]*Agroecology Institute, Göttingen University, Germany.*
[3]*Department of Biology, Tadulako University, Palu, Sulawesi, Indonesia.*
[4]*Department of Landscape Ecology, Göttingen University, Germany.*
[5]*Department of Biology, Bogor Agricultural University, Indonesia.*

In press: *Biotropica* 2010

ABSTRACT

Tropical secondary forest and agroforestry systems have been identified as important refuges for the local species diversity of birds and other animal groups, but little is known about the importance of these systems for terrestrial herbs. In particular, few studies report how the conversion from tropical forest to technified cacao plantation affect the species richness and the community structure of herbs. We conducted surveys in 43 cacao plantations along the border of the Lore Lindu National Park in Central Sulawesi, ranging from agroforests to technified cacao, categorizing the plantations as rustic cacao, planted shade cacao and technified cacao. We recorded 91 herb species. Of the 74 species determined to species level, 21 were also found in natural forests, while 53 were recorded only in agricultural habitats. Araceae was the most forest-dependent plant family while Asteraceae included the highest number of non-forest species. Overall, the presence of forest species was confined to moderately intensively managed rustic and planted shaded plantations. Distance from the forest, which has been identified as a crucial parameter for the diversity and composition of other taxa in cacao agroforests, only played a minimal role for herbs. Our study suggests that native forest herbs maybe more vulnerable to forest conversion than other plant and animal groups. The intensification of cacao plantation management increases the presence of weedy species to the detriment of native forest species.

Key words: Cacao, terrestrial herbs, tropical forest, Sulawesi.

INTRODUCTION

In the face of ongoing tropical forest destruction and degradation, secondary forests and agroforestry systems are becoming increasingly important habitats for tropical biodiversity (Perfecto *et al.* 2008). Cacao and coffee plantations, in particular, often retain a tall canopy of mixed tree species and are therefore considered to structurally resemble natural forests to some degree, providing important habitats for birds (Sodhi *et al.* 2005, Clough *et al.* 2009), amphibians and reptiles (Wanger *et al.* 2009), bats (Faria *et al.* 2006), bryophytes (Ariyanti *et al.* 2008), and trees (Zapfack *et al.* 2002, Sambuichi *et al.* 2007). However, different animal and plant groups react differently to habitat factors and are therefore represented idiosyncratically in agroforestry systems (Steffan-Dewenter *et al.* 2007, Kessler *et al.* 2009). A full assessment of the conservation potential of agroforestry systems thus needs to account for as many taxonomic and ecological groups as possible.

Ground-living herbaceous plants have so far largely been ignored in biodiversity assessments of agroforestry systems, even though herbs can make up a considerable proportion of plant diversity in tropical forests (Gentry & Dodson 1987) and also provide food or structural habitats for a wide range of animals (Höhn *et al.* 2009, Bos *et al.* 2007, Wanger *et al.* 2009). Furthermore, herbs may act as direct competitors to cultivated plants and act as reservoirs for pathogens and herbivores (Entwistle 1972, Siebert 2002). To our knowledge, herbs in cacao agroforestry systems have only been cursorily studied in Brazil (Faria *et al.* 2007), Cameroon (Bobo *et al.* 2006), and Indonesia (Ramadhanil *et al.* 2008, Steffan-Dewenter *et al.* 2007). These studies have shown that the abundance and diversity of terrestrial herbs is often higher in

agroforestry systems than in natural forests. However, many herbaceous plants in agricultural systems are widespread, weedy, and often alien species (Backer 1973), and the conservation value of agroforestry systems to native species is unknown. The importance of flowering herbaceous plants has not been explicitly studied in cacao plantations, though their importance for increasing the presence and diversity of pollinators has been documented in coffee plantations (Klein *et al.* 2003).

The composition and diversity of biotic communities in agroforestry systems depends on a wide range of factors, including distance from natural forest (Perfecto & Vandermeer 2008), management practices (Bos *et al.* 2007a, Ariyanti *et al.* 2008, Philpott *et al.* 2008), canopy composition and structure (Perfecto & Vandermeer 2008). Distance from the natural forest has been often identified as an important parameter in determining the diversity and composition of the assemblages, suggesting that dispersal from the forest is crucial and that many populations found in the agroforestry systems may be non-self-sustaining sink populations (Sambuichi *et al.* 2007, Sonwa *et al.* 2007, Sporn *et al.* 2007). Plantations with cultivated and native trees have been highlighted as ecosystems which harbor a variety of niches suitable for several groups of animals (Faria *et al.* 2007, Abrahamczyk *et al.* 2008, Wanger *et al.* 2009, Höhn *et al.* 2009). Cacao intensification alters tree species composition (Rice *et al.* 2000), modifying light intensity and air humidity, and consequently changing the ecological characteristics which in turn affect the abundance and community composition of ants (Kaspari *et al.* 2000, Philpott & Armbrecht 2006).

Cacao agroforestry systems can be divided into three management groups: rustic cacao, planted shade cacao and technified cacao (Rice *et al.* 2000). The so called "rustic cacao", which

occurs in many tropical countries, is characterized by cacao trees planted beneath thinned primary or old secondary forest. The next level of intensification is "planted shade cacao", which are traditional polycultural systems with mostly planted shade trees for timber or local fruit production. In our specific study, this category presents at least five species of planted trees in an area of 2500 m². The last category is "technified cacao", where the shade is provided by one or few planted species (Table 1). These are usually fast-growing, nitrogen-fixing legumes such as *Cassia*, *Gliricidia* and *Erythrina*. Final management intensification leads to the removal of trees for full sun production. A similar vegetation management gradient, ranging from the presence of tropical forest trees to planted monocultures has been also documented in coffee (Perfecto & Snelling 1995, Moguel & Toledo 1999).

The Malaysian region, located between mainland Asia and Australia, contains one of the richest tropical rainforest ecosystems, with over 41,000 vascular plant species recorded (Myers *et al.* 2000, Roos *et al.* 2004, van Welzen *et al.* 2005). Deforestation rates in the region exceed 1% per year (Laurance 2007), and in Indonesia even increased from 2.3% during the period 1990-2000 to 2.7% in 2000-2005 (Koh 2007). A large part of forest conversion in Indonesia is for the establishment of oil palm plantations, but forest conversion to cacao plays a large role in certain regions (ICCO 2008). Currently, Indonesia is the third largest cacao producer in the world (ICCO 2008). Within Indonesia, Sulawesi is a mid-sized island, composed of four peninsulas with a wide variety of geological substrates and vegetation types (Cannon *et al.* 2007). Over 5,000 vascular plant species, including 2,100 woody species of which almost 15% are endemic, have been recorded on the island so far (Kessler *et al.* 2005, Cannon *et al.* 2007, Culmsee &

Pitopang 2009). Botanical collecting intensity is very low and geographically uneven, so that many more species are expected to occur, and no species list of herbs is available at present.

This paper explores the diversity and composition of herb assemblages in cacao plantations in two valleys surrounding Lore Lindu National Park in Central Sulawesi (Fig. S1). The main objectives were to determine (a) the taxonomic composition and diversity of herb flora in the cacao plantations, (b) which local and landscape variables influence the composition and diversity of the herb assemblages, (c) the contribution of forest and open country species to the above patterns, and (d) the role of cacao agroforestry systems for the conservation of native herbaceous forest species in the study region.

STUDY SITE

The study was conducted in the Kulawi and Palolo valleys, at the northern and the western sides, respectively, of Lore Lindu National Park, Central Sulawesi (Fig.S1). Elevations of the study sites range from 400 m to 1000 m. Climatic seasonality is not pronounced, with a monthly average of over 100 mm of rainfall, although in some years monthly values can be far lower (Whitten *et al.* 1987). Minimum temperatures range between 12°C and 17°C, while maximum values range from 26°C to 35°C. The natural vegetation in the study area is evergreen tropical forest dominated by the families Anacardiaceae, Burseraceae, Guttifereae, Lauraceae, and Sapotaceae (Whitmore & Sidiyasa 1986, Kessler *et al.* 2005, Culmsee & Pitopang 2009). Logging is common outside and on the margins of the national park and has led to widespread deforestation and forest degradation (Belsky 2003). More than 7500 hectares of cacao

plantations have been established in and around the national park starting in the 1980s (Erasmi *et al*. 2004). Shade trees in the cacao plantations are either remnant trees from the native forest, mixed stands of planted trees such as candlenut *Aleurites moluccana* (L.) Willd., rambutan *Nephelium lappaceum* L., avocado *Persea americana* Mill., langsat (longan) *Lansium domesticum* Correa, and durian *Durio zibethinus* Rumph. ex Murray, or species-poor stands of the leguminous trees *Gliricidia sepium* (Jacq) Kunth ex Walp. and *Erythrina subumbrans* (Hassk.) Merr. (Kessler *et al.* 2005).

FIELD SAMPLING

Plantations were distributed across two valleys (22 in Kulawi and 21 in Palolo) differing in shade intensity and shade tree composition, as well as distance from the forest margin and elevation (Table 1), so that the full range of environmental factors was covered (Clough *et al.* 2009). In each plantation we established two 40 m x 40 m plots, which were rented from the farmers. Within each such plot we set apart a 5 m x 5 m plot for our herb survey. We sampled all the herbaceous plants in the study plots in October and November 2007.

	Number of plots	Planted fruit trees	Forest trees	Distance from the forest (m)	Elevation (m)
Rustic Cacao	12	5.6±3.4 ab	8.25±2.24 a	291±388 a	704±150 a
Planted shade cacao	17	7±3.13 a	2.5±3.9 b	351±350 a	657±127 a
Technified cacao	14	3.7 ± 1.38 b	1.9 ±2.63 b	560±598 a	636±102 a

TABLE 1. Number of planted and forest trees in the three cacao management categories. Significant differences are marked by different letters (ANOVA with Tukey post hoc test).

All terrestrial herb species were recorded and average height and total cover (in classes: 0-1%, 1-5%, 5-10%, 10-20%, 20-40%, 40-60%, 60-80%, 80-100%) estimated. Voucher specimens were collected for all species with at least seven duplicates and deposited in Herbarium Celebense, Palu (CEB), Herbarium Bogoriense, Bogor (BO), and the herbaria of Göttingen (GOET), Leiden (L), Zürich (Z), and UC Berkeley (UC, ferns only). Identifications were done at the herbaria of Göttingen (GOET) and Leiden (L); species difficult to determine were sent to specialists for identification. Information on species distribution was obtained from the Flora Malesiana Series (e.g., 1981, 1991, and 1998), from the botanical database Tropicos (www.tropicos.org) and the online herbarium of Leiden (http://www.nationaalherbarium.nl/virtual/).

In each plot we recorded the following environmental variables: elevation, slope, distance to natural forest and to the nearest river, and tree species number. Soil samples were collected at the edge of each plot and analyzed for a wide range of parameters. The cacao canopy cover was measured via hemispherical photographs taken with a digital camera with fisheye lens placed in

the center of each plot at approximately 50 cm above the ground; the surface captured by the fish lens was more than 70% of the plot.

DATA SAMPLYNG

Analyses were conducted for all herb species and for forest and non-forest herb species separately. Forest species were defined as species that also occur in natural forests, based on our exhaustive regional sampling of almost 200 study plots at a forest site at 1000 m asl in Kulawi valley (120° 3' 25.169" E 1° 30' 35.838" S) and a smaller number of plots in Palolo valley (Cicuzza *et al*. 2010). These plots were comparable in elevation with the study sites in the agroforestry systems.

Sampling completeness of herbs was evaluated using four species-richness estimators: Chao2, first- and second-order jackknife, and bootstrap (Herzog *et al.* 2002, Chiarucci *et al*. 2003). Sampling was too incomplete both in the cacao plantations and in the forest to calculate the overlap of species between both habitat categories. We therefore accounted for incomplete sampling using the Chao-Jaccard similarity index (Chao *et al.* 2005) as implemented in Estimates*S* (Colwell 2008) using presence-absence data.

A set of 18 environmental explanatory variables including eight soil factors, seven climatic factors, and three landscape variables were tested to explain herb diversity. These environmental explanatory variables were subjected to a Principal Component Analysis (PCA) to reduce the number of parameters, keeping those parameters separate that were not highly inter-correlated. Multiple regression models were then calculated with the PCA axes and the separate

explanatory variables to assess the most closely associated herb species community compositions. We used the Akaike's Information Criterion (AIC) to assess the goodness of fit of the estimated statistical models. Finally, an Indicator Species Analysis (Dufrene & Legendre 1997) was conducted to assess if individual herb species were associated with the three cacao agroforest types. Analyses were conducted in R (R Development Core Team 2007), with additional functions provided by the R package vegan (Oksanen *et al.* 2007). The Indicator Species Analysis was conducted with PCOrd 5.0 (McCune *et al.* 1999).

RESULTS

In total, we recorded 91 herb species in the 43 plots (Table S2), 74 of which were identified at the species level. The four species richness estimators applied suggest that between 72% and 89% of the regional herb species richness in all agroforestry systems was recovered by our samples (Chao2: 114±12 species; first-order jackknife: 114±5; second order jackknife 127±10; bootstrap 102±5) (Fig. 1B). Species numbers per plot varied from two to 25, with a mean of 13±5 species (Fig. 1A). Nineteen of the species had also been recorded in nearby natural forests (Cicuzza *et al.* 2010), resulting in a Classic Jaccard Similarity Index of 0.08. When taking into account sampling incompleteness, this value increased to 0.09 with the Chao-Jaccard-Raw Abundance-based Similarity Index and to 0.11 with the Chao-Jaccard-Estimated-Abundance-based Similarity Index.

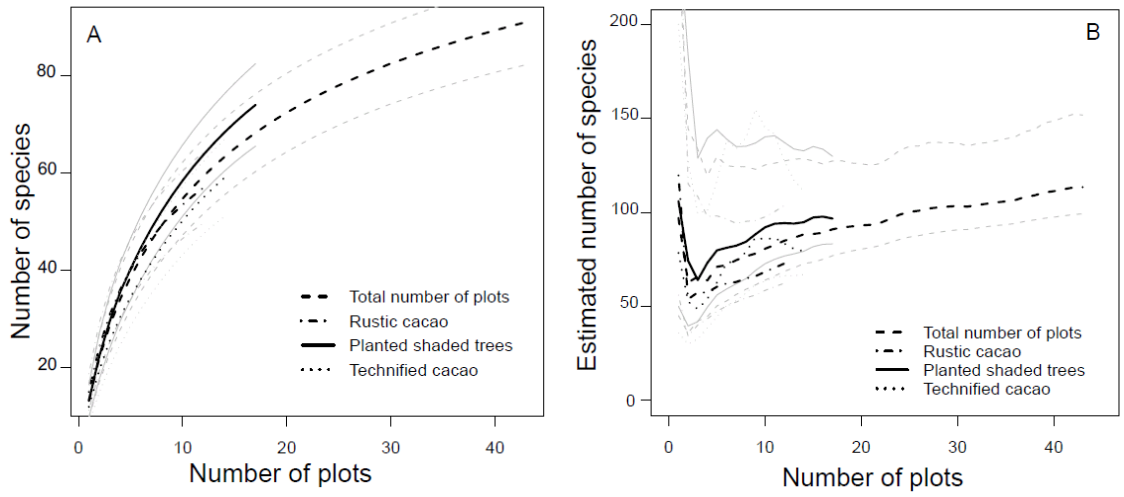


FIGURE 1. (A) Rarefied species density curves of the herbaceous species and (B) estimation of total species numbers using the Chao 2 richness estimator. Black curves represent the mean values of the three different cacao management categories ("rustic cacao", "planted shade cacao" and "technified cacao"), and the number of species for all plots combined, gray curves show the respective upper and lower 95% confidence intervals.

Overall, the most species-rich herb families were Asteraceae with 13 species followed by Araceae (10 species), Poaceae and Commelinaceae (9 species each). The ferns and lycophytes were represented by 15 species. In terms of ground cover, grasses of the family Poaceae (49%) were most dominant, followed by Asteraceae (18%), Commelinaceae (5%), and Araceae (3%). Ferns and lycophytes contributed 18% to ground cover. Of the 74 identified species, 21 (28%) species were also recorded in natural forests. This included five of the six species for Araceae and nine of the 15 species of ferns and lycophytes. The other seven species occur sporadically only in the tropical forest and not in the agroforestry systems. By contrast, all the species of the families Asteraceae, Commelinaceae, and Poaceae were non-forest species.

The PCA with the 18 explanatory variables resulted in four main axes including 12 factors, leaving additional six factors (cacao canopy cover, Simpson index of tree similarity, distance from the forest, slope, air humidity, valley identity) as individual variables for further analyses (Table S1). The four PCA axes together included 81% of the original variation. The first axis was correlated with elevation and three temperature variables (mean, minimum and maximum) explaining 32%. The second axis was related to soil factors (pH, C/N $CaCl_2$ and water soil content) and explained 22%. The third axis included soil micronutrients (Mg, Na) and 14% of the information. Finally, the fourth axis was correlated with light intensity below and above the cacao canopy and included 11% of the variation.

The final multiple regression model for the total number of herb species per plot accounted for 55% of the total variance and included four variables: cacao canopy cover, slope, Simpson tree diversity, and the PCA axis 1, which included the elevation influence (Table 2, Table 3, Fig. S2).

	Estimate	Standard Error	T value	Pr(>|t|)
	Total species			
Cacao Cover	-0.149	0.038	-3.977	<0.001
Tree Simpson diversity	6.839	2.948	2.320	0.026
Log (Inclination)	0.841	0.523	1.608	0.116
PC1	-1.600	0.894	-1.790	0.081
	Forest species			
Tree Simpson diversity	2.850	1.231	2.316	0.026
Log (Inclination)	0.464	0.220	2.104	0.042
PC1	-0.992	0.377	-2.635	0.012
	Non-forest species			
Cacao Cover	-0.080	0.034	-2.353	0.024
Log (Inclination)	0.570	0.418	1.364	0.180
PC4	1.633	0.818	1.996	0.053

TABLE 2. Results of the multiple regression analyses of the number of herb species against ten environmental variables. Only those variables kept in the model after stepwise exclusion of redundant variables are listed.

Explanation %	34.2	21.8	13.8	11.1
	PC1	PC2	PC3	PC4
Altitude	**-1.144 *** **	0.454	-0.015	0.253
Light intensity (1.30 m)	0.389*	-0.091	0.066	**1.067 *** **
Light intensity (5.80m)	0.577 **	-0.088	-0.409 *	**0.927 *** **
Temperature, Max	**1.120 *** **	-0.542	-0.241	0.054
Temperature, Mean	**1.175 *** **	-0.554	-0.078	-0.140
Temperature, Min	**1.080 *** **	-0.493	0.170	-0.508 *
C/N	0.122	**-0.960*** **	-0.129	0.197
Mg [mg/g]	0.032	-0.391	**1.158 *** **	0.182
Na [mg/g]	-0.115	-0.217	**1.216 *** **	0.239
Soil Water content	-0.646	**-0.961 *** **	0.011	-0.212
pH	**-0.941 *** **	**-0.632 *** **	-0.236	0.120
$CaCl_2$	-0.672	**-0.853 *** **	-0.288	0.196

TABLE 3. Results of the Principal Component Analysis based on the 12 environmental factors; the four first PCA axes together include the 81% of the original variation. Bold numbers show the factors most strongly correlated to the individual PCA axes. (*P <0.05, **P <0.01, ***P <0.001).

The multiple regression model analysis for forest herbs only explained 62% of the total variance and included three variables: slope, Simpson tree diversity and the first PCA axis (Fig. S3). Among these variables the first PCA axis and the Simpson index of tree species were highly significant. The multiple regression model for the non-forest species explained 54% of the variance and included cacao canopy cover, the Simpson tree diversity index, and the fourth PCA axis including light information. Only the cacao canopy cover and the fourth PCA axis were significantly correlated with the non forest species.

The Indicator Species Analysis found that 16 species were significantly associated with one of the three cacao agroforest types we defined previously (Table 4). The number of characteristic forest species decreased from the rustic to the legume-dominated cacao plantations, while the non-forest species showed the opposite trend. The four identified species typical for rustic cacao plantations included one that is endemic to Sulawesi, two with Malaysian distribution, and only one pantropical species. The mixed shade planted plantations included two species with a wide South East Asian distribution, one species with Malaysian distribution and two pantropicals; while the technified cacao had four species with pantropical distribution.

Rustic cacao	**Planted shade trees**	**Technified cacao**
15±1	13±1	12±1
Pothos tener Wall. (Arac.) F * (I)	*Asplenium nidus* L. (Asplen.) F * (P)	Zingiberaceae gen. sp. F *
Musa celebica Warb. ex K. Schum. (Musac.) F * (E)	*Elatostema papangae* Leandri (Urticac.) F * (M)	*Hyptis capitata* Jacq. (Lam.) N* (P)
Trichosanthes trifolia (L.) Merr. (Cucurb.) F ** (M)	*Cyrtococcum accrescens* (Trin.) Stapf. (Poac.) N * (SEA)	*Borreria laevis* (Rubiac.) N * (P)
Passiflora foetida L. (Passifl.) N * (P)	*Oplismenus compositum* (L.) P. Beauv. (Poac.) N * (SA)	*Christella parasitica* (L.) Lev. (Thelypterid.) N * (P)
Urticaceae gen. sp. N *	*Crassocephalum crepidioides* (Benth.) S. Moore (Aster.) N * (P)	*Elephantopus scaber* (Aster.) N * (P)
		Hygrophila sp. (Acanthac.) N *

TABLE 4. Species numbers and characteristic species for the three cacao management categories. F = Forest species, N = Non-forest species. In parenthesis are specified the species distribution and the family; I = Indonesia, E = Endemic, M = Malaysian Archipelago, SEA = South East Asia, SA = South Asia, P = pantropical. (*P<0.01, **P<0.05).

DISCUSSION

Overall, we found 91 terrestrial herb species in the 43 cacao agroforestry systems. This is lower than the 260 herbaceous species found by Bisseleua *at al.* (2008) in traditional cacao forest gardens in Cameroon. Taxonomic composition also differed between the study regions, with the most common families in Cameroon being Acanthaceae (23 species), Commelinaceae (12), Poaceae (10), Araceae (8), Rubiaceae (6), and Asteraceae (4), and in our study Poaceae, Asteraceae and Araceae. In Brazilian cabruca cacao agroforestry systems, Faria *et al.* (2007) recorded 41 fern species, which is considerably more than the 15 species that we found. Thus, cacao agroforestry systems in our study region appear to be less species rich than in many other geographical areas, although differences in sampling area and methodology make a direct comparison of species numbers difficult.

Comparing the number of herb species in agroforestry systems and adjacent natural forests, Cicuzza *et al.* (2010) found 171 and 203 species in two forest sites close to the agroforestry systems studied here, revealing much higher herb species richness in the tropical forest. In their study, ferns and lycophytes alone contributed 94 and 112 species, which is almost ten times higher as in the cacao agroforestry systems. In contrast, Faria *et al.* (2007) only found 51 fern and lycophyte species in natural forests adjacent to cacao plantations in Brazil, which supported 41 species. This suggests that there may be geographical differences in the proportion of forest herbs than can be found in cacao agroforestry systems.

We found that in our study area, agroforestry systems and natural forests had largely distinct herb community. The three levels of management intensity in the cacao plantations did not differ systematically in their species richness (Fig. 2) or species composition (Fig. S2). To our knowledge, farmers do not target individual herb species during management, but rather cut or apply herbicides to the entire plantation. Herb communities in the cacao agroforestry system were primarily composed of widespread weedy species whose conservation value is low but which might play important ecological roles in the agroforestry systems. Their richness was significantly correlated with cacao canopy cover and the fourth PCA axis, variables which are ecologically related with light intensity are often documented has a key variables for the spread of weedy species (Chen *et al.* 2009). Weedy herbs can reduce the capability of regeneration for local natural species (Wong *et al.* 2010). The grass *Imperata cilindrica* (L.) Beauv., were presented in eight (15%) of our plots, seem to be an aggressive invasive that it often tends to reach 100% cover in disturbed sites (Holly *et al.* 2006). A second weedy Poaceae in our study system is *Paspalum conjugatum* P.J. Bergius, native from South Africa, which is frequently used in private or public gardens and parks in Indonesia. Through its robust rhizome system this species reduces soil erosion and improves humus quality and soil nutrients in coffee plantations, but it may also competitively exclude other herb species (Afanti *et al.* 2002; Watanabe *et al.* 2007). In our area, this species was present in 31 (70%) of the plots. Another African weed is the Asteraceae *Crassochepalum crepidioides* (Benth.) S. which is also a minor vegetable (Ismail *et al.* 2001; Dairo & Wright 2007). We recorded this Asteraceae in 24 (55%) of our plots. During the flowering period, this species might attract insects, which can play a role for the pollination of the shrubs and fruit tree species planted in the cacao agroforestry system (Klein *et al.* 2003).

However, for this species as for all other weedy species, we have no direct evidence of any ecological significance in the study region.

Focusing more on the native herb flora of conservation concern, only 28% of the herb species in the cacao plantations were also recorded in the adjacent forests (Cicuzza *et al.* 2010), a value that was only marginally influenced by sampling incompleteness. Beyond this main distinction between natural forests and agroforestry systems, there was also considerable variation among different agroforest types, depending on local site conditions and management intensity. We found that the number of herb species was higher in plots with high tree diversity and at high elevations, while the further separation into forest and non-forest species showed that richness of the former also increased on plots with high slope inclination and of the latter in plantations with low cacao canopy cover and high light intensity. Therefore, elevation and presence of native forest tree species appear to determine the importance of a cacao plantation for the conservation of native herbaceous species. These conditions are not necessarily found adjacent to the forest margin, as evidenced by the fact that the distance from the forest was not recovered as a significant variable in our analysis. Rather, it is the management intensity of the plantation that plays the crucial role. Comparing differently managed cacao plantations, we found that each had different suites of herb species, with rustic plantations having a constant presence of forest-dependent and often geographically localized species whereas more intensively managed plantations were characterized by weedy, pantropical taxa.

These results make intuitive sense and show that populations of natural forest herbs are mostly found in rustic plantations. First, the vegetation structure of these plantations is comprised of a relatively dense canopy made up by natural forest trees, which is most similar to

that of natural forests. Furthermore, since they have been converted to plantations only fairly recently, it is probable that part of the herb individuals found in such plantations belong to the original forest herb flora. This is supported by our observation that only three (11%) of the forest species recorded in rustic plantations were found in reproductive condition (Cicuzza *et al.* pers. obs.).

In summary, we conclude that despite high species richness of herbs, cacao agroforestry systems of medium and high management intensity are of very limited value for the conservation of native forest species in the Kulawi and Palolo valleys in central Sulawesi, Indonesia. A pattern of decreasing species richness in more intensively managed agroforestry systems has been documented in our study area for trees (Steffan-Dewenter *et al.* 2007), bryophytes (Ariyanti *et al.* 2008, Sporn *et al.* 2007), canopy-inhabiting ants (Bos *et al.* 2007), and for trees elsewhere (Sambuichi *et al.* 2007, Sonwa *et al.* 2007). In contrast, a relatively high conservation value of cacao agroforestry systems has been found for birds (Abrahamczyk *et al.* 2008, Clough *et al.* 2009), reptiles and amphibians (Wanger *et al.* 2009), and various insect groups (Bos *et al.* 2007, Höhn *et al.* 2009) in our study region, and for ferns, frogs, lizards, birds and bats in Brazil (Faria *et al.* 2007). We conclude that although secondary forests and agroforestry systems are often considered important ecosystems for biodiversity conservation in countries where most natural forest has been lost (, Wright 2006, Dent & Wright 2009), cacao agroforestry systems in our study region are of limited conservation value for terrestrial herbs.

ACKNOWLEDGMENTS

This study was funded by the German Research Foundation (DFG), grant SFB-552 STORMA (Stability of Rainforest Margins) www.storma.de. Herb species identification was conducted partly at the Herbarium of Leiden (The Netherland) supported by Synthesys NL-TAF 3536. We thank to Stefan Couler Laboratory director of the Palu University. We thank Adam Malik, Wolfram Lorenz, Surya Tarigan, Muhammad Sigit and all plantation owners for their help in this work.

LITERATURE CITED

ABRAHAMCZYK, S., M. KESSLER, D. PUTRA, M. WALTERT, AND T. TSCHARNTKE. 2008. The value of differently managed cacao plantations for forest birds conservation in Sulawesi, Indonesia. Bird Conservation International 18: 349-362.

AFANTI, T. K. MANIK, B. ROSANDI, M. UTOMO, M. SENGE, T. ADACHI AND Y. OCHI. 2003. Soil erosion under coffee with different weed managements in humid tropical hilly area of Lampung, south Sumatra, Indonesia. J. Jpn. Soc. Soil Phys. 9: 3-14.

ARIYANTI, N. S., M. BOS, K. KARTAWINATA, S. S. TJITROSOEDIRDJO, E. GUHARDJA. AND S. R. GRADSTEIN. 2008. Bryopytes in tree trunks in natural forests, selectively logged forests and cacao agroforests in Central Sulawesi, Indonesia. Biol. Conserv. 141: 2516-2527.

BACKER, C. A. 1973. Atlas of 220 weeds of sugar cane fields in Java. *In* BACKER, C. A. (Ed.). Indonesian Sugar Experiment Station Pasuruan, Indonesia.

BISSELEUA D., HERVÉ, B., AND STEFAN, V. 2008. Plant biodiversity and vegetation structure in traditional cocoa forest gardens in southern Cameroon under different management. Biodivers. Conserv. 17: 1821-1835.

BOBO K. S., M. WALTERT, N. M. SAINGE, J. NJOKAGBOR, H. FERMON, AND M. MÜHLENBERG. 2006. From forest to farmland: species richness patterns of trees and understory plants along a gradient of forest conversion in Southwestern Cameroon. Biodivers. Conserv. 15: 4097-4117.

BOS, M. M., P. HÖHN, S. SALEH, B. BÜCHE, D. BUCHORI, I. S. DEWENTER, AND T. TSCHARNTKE. 2007. Insect diversity responses to forest conversion and agroforestry management. *In* Tscharntke T., C. Leuschner, M. Zeller, E. Guhardja, A. Bidin. (Eds.). The stability of tropical rainforest margins, linking ecological, economic and social constraints of land use and conservation, pp. 279-296. Springer, Berlin.

BOS, M. M., I. S. DEWENTER, AND T. TSCHARNTKE. 2007a. The contribution of cacao agroforests to the conservation of lower canopy ant and beetle diversity in Indonesia. Biodivers. Conserv. 16: 2429-2444.

BELSKY, J. M., AND S. F. SIEBERT. 2003. Cultivating cacao: Implications of sun-grown cacao on local food security and environmental sustainability. Agr. Human Values 20: 277-285.

CANNON, C., H. SUMMERS M., J. R. HARTING, AND P. J. A. KESSLER. 2007. Developing conservation priorities based on forest type, condition, and threats in a poor known ecoregion: Sulawesi, Indonesia. Biotropica 39: 747-759.

CHAO, A., R. L. CHAZDON, R. K. COLWELL, AND T. J. SHEN. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol. Lett. 8: 148–159.

CICUZZA, D., M. KESSLER, R. PITOPANG, S. S. TJITROSOEDIRDIO, AND S. R. GRADSTEIN. 2010. Terrestrial herb of tropical submontane and tropical montane forests in Central Sualwesi, Indonesia. *In* T. Tscharntke, C. Leuschner, E. Veldkamp, H. Faust, E. Guhardja, A. Bidin. (Ed.). Tropical rainforest and agroforests under global change, pp. 378-390.

CHIARUCCI, A., N. J. ENRIGHT, G. L. W. PERRY, B. P. MILLER, AND B. B. LAMONT. 2003. Performance of non parametric species richness estimators in a high diversity plant community. Divers. Distrib. 9: 283-295.

CHEN, G. Q., S. L. GUO, AND Q. S. HUANG. 2009. Invasiveness evaluation of fireweed (*Crassocephalum crepidioides*) based on its seed germination features. Weed Biol. Manag. 9: 123-128.

CLOUGH, Y., D. DWI PUTRA, R. PITOPANG, AND T. TSCHARNTKE. 2009. Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry. Biol. Conserv. 142: 1032-1041.

COLWELL, R. K. 2008. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.0.0 User's guide and application. Available at: http://purl.oclc.org/estimates

CULMSEE, H., AND R. PITOPANG. 2009. Tree diversity in sub-montane and lower montane primary rain forest in Central Sulawesi. Blumea 54: 119-123.

DAIRO F. A. S. AND ADANLAWO I. G. 2007. Nutritional quality of *Crassocephalum crepidioides* and *Senecio biafrae*. Pak. J. Nutr. 6: 35-39.

DENT, D. H., AND S. J. WRIGHT. 2009. The future of tropical species in secondary forests: A quantitative review. Biol. Conserv. 142: 2833-2843.

DUFRENE, M., AND P. LEGENDRE. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67: 345-366.

ENTWISTLE, P. F. 1972. Pests of cocoa. Longman, London, UK.

ERASMI, S., A. TWELE, M. ARDIANSYAH, A. MALIK, AND S. M. KAPPAS. 2004. Mapping deforestation and land cover conversion at the rainforest margin in Central Sulawesi, Indonesia. EARSeL e Prooceedings. 3: 388-397.

FARIA, D., R. R. LAPS, J. BAUMGARTEN, AND M. CETRA. 2006. Bat and birds assemblages from forests and shade cacao plantations in two contrasting landscape in the Atlantic Forest of southern Bahia, Brazil. Biodivers. Conserv. 15: 587-612.

FARIA, D., M. L. B. PACIENCIA, M. DIXO, R. R. LAPS, AND J. BAUMGARTEN. 2007. Ferns, frogs, lizards, birds and bats in forest fragments and shade cacao plantations in two contrasting landscapes in the Atlantic Forest, Brazil. Biodivers. Conserv. 16: 2335-2357.

FLORA MALESIANA, PTERIDOPHYTA (Ferns and Ferns Allies). 1981. Vol. 1. National Herbarium Nederland Univeriteit, Leiden branch. The Netherlands.

FLORA MALESIANA, PTERIDOPHYTA (Ferns and Ferns Allies). 1991. Vol. 2. National Herbarium Nederland Univeriteit, Leiden branch. The Netherlands.

FLORA MALESIANA, PTERIDOPHYTA (Ferns and Ferns Allies). 1998. Vol. 3. National Herbarium Nederland Univeriteit, Leiden branch. The Netherlands.

GENTRY, A. H., AND L. H. EMMONS. 1987. Geographical variation in fertility phenology and composition of the understory of neotropical forest. Biotropica 19: 216-227.

HERZOG, S. K., M. KESSLER, AND T. M. CAHILL. 2002. Evaluation of a new rapid assessment method for estimating avian diversity in tropical forests. The Auk 199: 749–769.

HÖHN, P., I. S. DEWENTER, B. DAMAYANTI, AND T. TSCHARNTKE. 2009. Spatiotemporal density patterns of the pest predator *Rhynchium haemorrhoidale* (F.) along a land-use gradient in cacao agroforestry systems. Agroforest Syst. 76: 163-171.

HOLLY, D.C., AND G.N. ERVIN. 2006. Characterization and quantitative assessment of interspecific and intraspecific penetration of belowground vegetation by cogongrass (*Imperata cylindrica* (L.) Beauv.) rhizomes. Weed Biol. Manage. 6:120-123.

ICCO. 2008. Production of cocoa beans. Quarterly Bullettin of Cocoa Statistics (ICCO) 43.

ISMAIL, B. S., S. CHUAH, S. SALMIJAH, AND K. H. HUSSIN. 2001. Role of superoxide dismutase and peroxidase activities in paraquat resistant redflower ragleaf (*Crassocephalum crepidioides* (Benth.) S. Moore). Aust. J. Agric. Res. 52: 583-586.

KASPARI, M., AND M. D. WEISER. 2000. Ant activity along moisture gradients in a neotropical forest . Biotropica 32: 703–711.

KESSLER, M. S., ABRAHAMCZYK, M. BOS, D. BUCHORI, D. D. PUTRA, S. R. GRADSTEIN, P. HÖHN, J. KLUGE, F. OREND, R. PITOPANG, S. SALEH, C. H. SCHULZE, S. G. SPORN, I. STEFFAN-DEWENTER, S. S. TJITROSOEDIRDJO, AND T. TSCHARNTKE. 2009. Alpha and beta diversity of plants and animals along a tropical land-use gradient. Ecol. Appl. 19: 2142-2156.

KLEIN, A. M., I. STEFFAN-DEWENTER AND T. TSCHARNTKE. 2003. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. J. Veg. Sci. 40: 837-845.

KESSLER, M., P. J. A. KESSLER, S. R. GRADSTEIN, K. BACH, M. SCHMULL, AND R. PITOPANG. 2005. Tree diversity in primary forest and different land use systems in Central Sulawesi. Indonesia. Biodivers. Conserv. 14: 547-560.

KOH, L. P. 2007. Impending disaster or sliver of hope for Southeast Asian forest? The devil may lie in the details. Biodivers. Conserv. 16: 3935-3938.

LAURANCE, W. F. 2007. Forest destruction in tropical Asia. Curr. Sci. India 11: 1544-1550.

MC CUNE, B. AND M. J. MEFFORD. 1999. PC-ORD Multivariate analysis of ecological data. Version 5. MjM Software Design, Gleneden Beach OR

MOGUEL, P., AND TOLEDO V.M. 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conserv. Biol. 13: 11-21.

MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. DA FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

OKSANEN, J., R. KINDT, P. LEGENDRE, B. O'HARA, AND M. H. H. STEVENS. 2007. Vegan: Community Ecology Package. R package version 1.8-8 http://r-forge.r-project.org/project/vegan/.

PERFECTO, I., AND R. SNELLING. 1995. Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. Ecol. Appl. 5: 1084-1097.

PERFECTO, I., AND J. VANDERMEER. 2008. Biodiversity conservation in Tropical Agroecosystems, a new conservation paradigm. Ann. NY. Acad. Sci. 1134: 173-200.

PHILPOTT, S. M., AND I. ARMBRECHT. 2006. Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. Ecol. Entomol. 31: 369-377.

PHILPOTT, M. S., P. BICHIER, R. A. RICE AND R. GREENBERG. 2008. Biodiversity conservation, yield, and alternative products in coffee agroecosystems in Sumatra, Indonesia. Biodiv. Conserv. 17: 1805-1820.

RAMADHANIL, P., S. S. TJITROSOEDIRDJO, AND D. SETIADI. 2008. Structure and composition af understory plant assemblages of six land use types in the Lore Lindu National Park, Central Sulawesi, Indonesia. Bangl. J. Plant Taxon 15: 1-12.

R DEVELOPMENT CORE TEAM. 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org

RICE, R. A., AND R. GREENBERG. 2000. Cacao cultivation and the conservation of biological diversity. Ambio 29: 167-173.

ROOS, M. C., P. J. A. KESSLER, S. R. GRADSTEIN, AND P. BASS. 2004. Species diversity and endemism of five major Malesian islands: diversity-area relationships. J. Biogeogr. 31: 1893-1908.

SAMBUICHI, R. H. R., AND M. HARIDASAN. 2007. Recovery of species richness and conservation of native Atlantic forest trees in the cacao plantations of southern Bahia in Brazil. Biodivers. Conserv. 16: 3681-3701.

SIEBERT, S. F. 2002. From shade- to sun-grown perennial crops in Sulawesi, Indonesia: implications for biodiversity conservation and soil fertility. Biodivers. Conserv. 11: 1889-1902.

SONWA, D. J., B. A. NKONGMENECK, S. F. WEISE, M. TCHATAT, A. A. ADESINA, AND M. J. J. JANSSENS. 2007. Diversity of plants in cocoa agroforests in the humid forest zone of Southern Cameroon. Biodivers. Conserv. 16: 2385-2400.

SODHI, N. S., L. P. KOH, D. M. PRAWIRADILAGA, DARJONO, I. TINULELE, D. D. PUTRA, AND T. H. T. TAN. 2005. Land use and conservation value for forest birds in central Sulawesi (Indonesia). Biol. Conserv. 122: 547-558.

STEFFAN-DEWENTER, I., M. KESSLER, J. BARKMANN, M. M. BOS, D. BUCHORI, S. ERASMI, H. FAUST, G. GEROLD, K. GLENK, R. S. GRADSTEIN, E. GUHARDJA, M. HARTEVELD, D. HERTEL, P. HÖHN, M. KAPPAS, S. KÖHLER, C. LEUSCHNER, M. MAERTENS, R. MARGGRAF, S. MIGGE-KLEIAN, J. MOGEA, R. PITOPANG, M. SCHAFER, S. SCHWARZE, S. G. SPORN, A. STEINGREBE, S. S. TJITROSOEDIRDJO, S. TJITROSOEDIRDJO, A. TWELE, R. WEBER, L. WOLTMANN, M. ZELLER, AND T. TSCHARNTKE. 2007. Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. Proc. Natl. Acad. Sci. USA 12: 4973-4978.

SPORN, S. G., M. M. BOS, AND S. R. GRADSTEIN. 2007. Is productivity of cacao impeded by epiphytes? An experimental approach. Agricul. Ecosyst. Envir. 122: 490-493.

VAN WELZEN, P., F. J. W. SLIK, AND J. ALAHUHTA. 2005. Plant distribution patterns and plate tectonics in Malesia. Biol. Skript. 55: 199-217.

WANGER, T. C., A. SARO, D. T. ISKANDAR, B. W. BROOK, N. S. SODHI, Y. CLOUGH, AND T. TSCHARNTKE. 2009. Conservation value of cacao agroforestry for amphibians and reptiles in Southeast Asia: combining correlative models with follow-up field experiments. J. Appl. Ecol. 46: 823-832.

WATANABE, A., H. TAKADA, SARNO, AFANDI, T. ADACHI, Y. OKI, AND M. SENGE. 2007. Assessment of degradation and generation of humus in a coffee soil affected by weed cover by means of a stable carbon isotopic ratio. Eur. J. Soil Sci. 58: 1042-1049.

WHITMORE T.C., AND SAYER J.A. 1986. Composition and Structure of a Lowland Rain Forest at Toraut, Northern Sulawesi. Kew Bull. 41: 747-757.

WHITTEN, A.J., M. MUSLIM, AND G. S. HENDERSON. 1987. The Ecology of Sulawesi. Gadjah Mada University Press, Yogyakarta, Indonesia.

WONG, K. M., M. SUGUMARAN, D. K. P. LEE, AND M. S. ZAHID. 2010. Ecological aspects of endemics plant population on Klang Gates quartz ridge, a habitat island in Peninsular Malaysia. Biodivers. Conserv. 19: 435-447.

WRIGHT, S. J. 2006. The uncertain future of tropical forest species. Biotropica 38: 443-445.
ZAPFACK, L., S. ENGWALD, B. SONKE, G. ACHOUNDONG, AND B. MADONG. 2002. The impact of land conversion on plant biodiversity in the forest zone of Cameroon. Biodivers. Conserv. 11: 2047-2061.

SUPPORTING INFORMATION

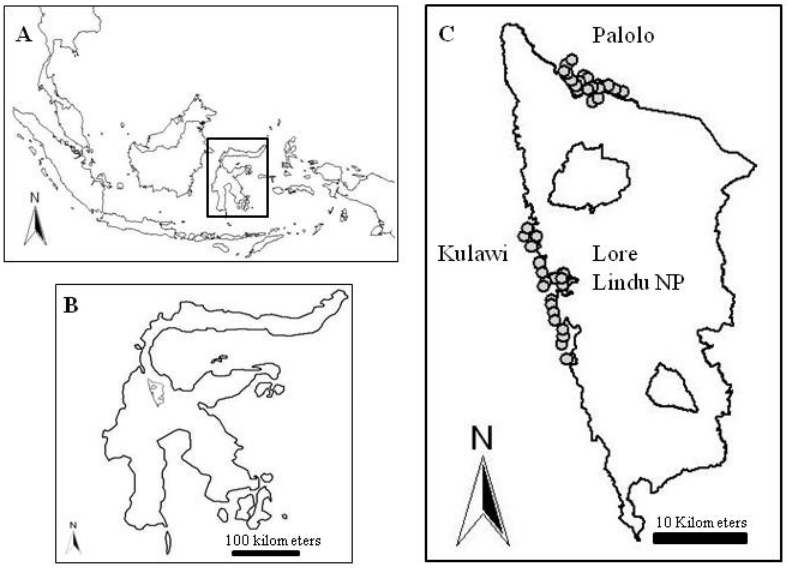


FIGURE S1. Maps of study area: (A) the Malay archipelago with the Sulawesi island higlighted; (B) Sulawesi with the location of the Lore Lindu National Park; (C) Lore Lindu National Park with the position of the 43 research plots (circles) in Palolo and Kulawi valleys.

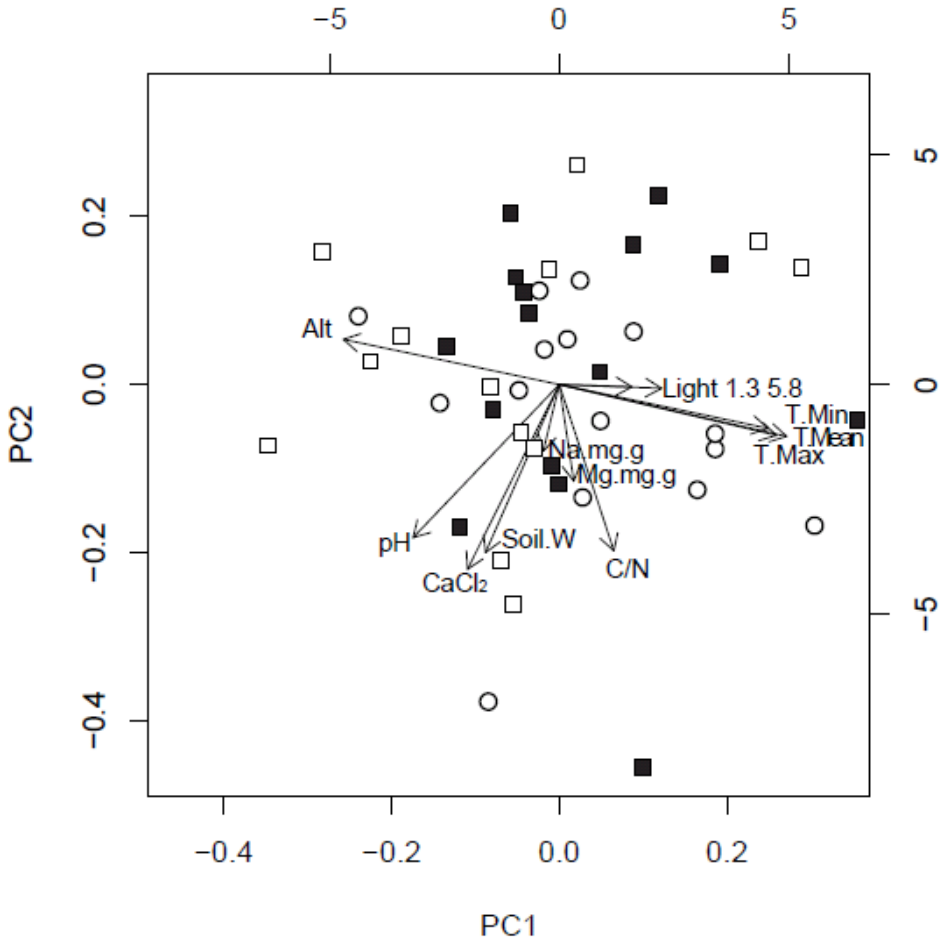


FIGURE S2. Principal Component Analysis of the 43 study plots relative to their species composition; open square: rustic cacao; open circle: planted shade cacao; solid square: technified cacao. The arrows show the relationship to the 12 environmental parameters listed in the Table 3.

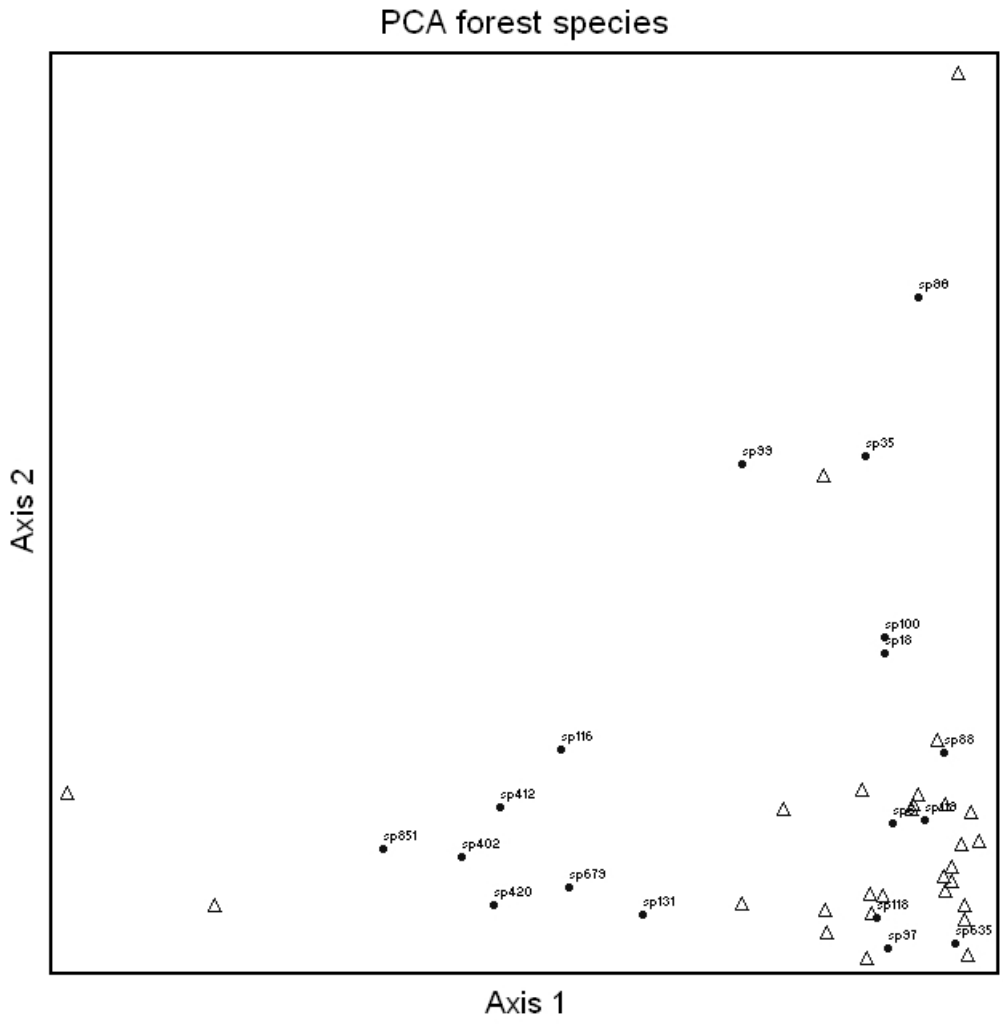


FIGURE S3. The Principal Component Analysis for the 19 forest-based species (circles), relative to their 43 plots (triangles).

	PC1	PC2	PC3	PC4	PC5	PC6
sp8	0.114	0.206	0.024	0.110	5.792	5.109
sp402	-4.667	-0.163	-0.885	0.620	-0.546	0.597
sp412	-4.251	0.388	-0.692	2.349	2.458	0.917
sp18	0.024	2.093	6.477	1.371	-1.775	1.757
sp35	-0.199	4.275	2.782	-0.452	0.757	-4.109
sp88	0.675	0.986	-1.670	-1.361	-2.073	0.293
sp89	0.391	6.010	-3.308	-0.876	-1.461	0.231
sp90	0.391	6.040	-3.308	-0.876	-1.461	0.231
sp97	0.051	-1.174	-0.120	-3.648	3.151	-0.175
sp99	-1.562	4.187	-0.257	1.938	4.241	2.594
sp100	0.016	2.281	4.609	0.663	1.795	-3.387
sp116	-3.576	1.032	3.510	-1.635	0.892	-1.873
sp118	-0.077	-0.834	-0.926	5.207	-1.443	-3.109
sp119	0.457	0.243	3.424	1.321	-3.966	6.030
sp635	0.803	-1.123	0.148	-2.811	3.085	-2.459
sp420	-4.324	-0.697	-0.551	-2.271	-0.417	0.497
sp131	-2.663	-0.804	-1.739	5.950	0.053	-1.877
sp679	-3.486	-0.490	0.322	-3.905	-3.612	-0.276
sp851	-5.538	-0.073	-0.265	-1.114	-0.826	0.459

TABLE S1. Results of the Principal Component Analysis based on the 19 herbaceous forest species and the six PCA axes obtained with the PCA analysis.

Family	Species	Distribution
Acanthaceae	*Blechum piramidatum* (Lam.) Urb.	America, Asia
Acanthaceae	*Hygrophila* sp. I	
Amaranthaceae	*Cyathula prostrata* (L.) Blume	Africa, Asia
Apiaceae	*Centella asiatica* (L.) Urb.	Pantropical
Araceae	*Aglaonema nitidum* (Jack) Kunth	Asia, Malay
Araceae	*Aglaonema simplex* (Blume) Blume	Indonesia
Araceae	*Alocasia balgooyi* H. Hay	Sulawesi
Araceae	*Amydrium zippellinum* (Schott) Nicholson	South East Asia
Araceaea	*Homalomena* sp. I	
Araceaea	*Scindapsus marantaefolius* Miq.	Indonesia
Araceae	*Schismatoglottis motleyana* (Schott) Engl.	Sulawesi
Araceae	*Scindapsus pictus* Hassk.	Asia, Malay
Araceaea	*Pothos tener* Wall.	Indonesia
Araceae	*Araceae* sp. I	
Aspleniaceae	*Asplenium macrophyllum* Sw.	South East Asia
Aspleniaceae	*Asplenium nidus* L.	Pantropical
Asteraceae	*Ageratum conyzoides* L.	America, Asia
Asteraceae	*Bidens pilosa* L.	America, Asia
Asteraceae	*Chromolaena odorata* (L.) R.M. King & H. Rob.	America, Asia
Asteraceae	*Crassocephalum crepidioides* (Beth.) S. Moore	Africa, Asia
Asteraceae	*Crassocephalus* sp. I	
Asteraceae	*Elephantopus scaber* L.	Pantropical

Asteraceae	*Emilia sonchifolia* (L.) DC.	South East Asia
Asteraceae	*Spilanthes paniculata* Wall. ex. DC.	Pantropical
Asteraceae	*Synedrella nodiflora* (L.) Gaertn.	America, Asia
Asteraceae	*Vernonia cinerea* (L.) Less.	Africa, Asia
Asteraceae	*Zinnia elegans* Jacq.	America, Asia
Asteraceae	*Asteraceae* sp. I	
Balsaminaceae	*Impatiens platypetala* var. *Aurantiaca* Steen	Indonesia
Balsaminaceae	*Impatiens platypetala* Lindl.	Indonesia
Balsaminaceae	*Impatiens platypetala* ssp. *platypetala*	Indonesia
Balsaminaceae	*Impatiens radicans* Zoll.	Indonesia
Campanulaceae	*Campanulaceae* sp. I	
Capparaceae	*Cleome rutidosperma* DC.	Africa, Asia
Cariophyllaceae	*Drymaria cordata* (L.) Willd. ex Roem. & Schult.	America, Asia
Commelinaceae	*Borreria* sp. I	
Commelinaceae	*Borreria* sp. II	
Commelinaceae	*Commelina benghalensis* L.	Pantropical
Commelinaceae	*Commelina difformis* L.	Indonesia
Commelinaceae	*Commelina diffusa* Zoll. Ex C. B. Clarke	Pantropical
Commelinaceae	*Cyanotis axillaris* (L.) Schult. f.	Asia, Malay
Commelinaceae	*Commelina* sp. I	
Convolvulaceae	*Convulvulacae* sp. I	
Convolvulaceae	*Ipomea batatas* (L.) Lam.	Pantropical
Costaceae	*Costus speciosus* (J. König) Sm.	Pantropical
Cucurbitaceae	*Trichosanthes tricuspidata* Lour.	Asia
Cyperaceae	*Cyperus cephalotes* Vahl	South East Asia
Cyperaceae	*Cyperus digitatus* Nees	Pantropical

Cyperaceae	*Cyperus elongate* Sieber ex Kunth	Pantropical
Cyperaceae	*Cyperus kyllingia* Endl.	Pantropical
Davalliaceae	*Davallia trichomanoides* Blume	Asia, Malay
Dennstaedtiaceae	*Hypolepis brooksiae* Alderw.	Indonesia
Dryopteridaceae	*Diplazium asperum* Blume	Asia, Malay
Dryopteridaceae	*Diplazium esculentum* (Retz.) Sw.	Pantropical
Euphorbiaceae	*Euphorbia heterophylla* L.	America, Asia
Hypoxidaceae	*Curculigo latifolia* (Dryand)	Africa, Asia
Lamiaceae	*Hyptis capitata* Jacq.	Pantropical
Lamiaceae	*Scutellaria javanica* Jungh.	Asia, Malay
Lamiaceae	*Lamiaceae* sp. I	
Leguminosaceae	*Calopogonium mucunoide* Desv.	America, Asia
Lomariopsidaceae	*Bolbitis appendiculata* (Willd.) K. Iwats	Asia, Malay
Marattiaceae	*Ptisana sylvatica* (Blume) Murdock	Asia
Musaceae	*Musa celebica* Warb. ex K. Schum.	Sulawesi
Nephrolepidaceae	*Nephrolepis biserrata* (Sw.) Schott	Indonesia
Nephrolepidaceae	*Nephrolepis falciformis* J. Sm.	Indonesia
Orchidaceae	*Orchidaceae* sp. I	
Oxalidaceae	*Oxalis corniculata* L.	Pantropical
Passifloraceae	*Passiflora foetida* L.	Pantropical
Poaceae	*Axonopus compressus* (Sw.) P. Beauv.	America, Asia
Poaceae	*Centotheca lappacea* (L.) Desv.	Pantropical
Poaceae	*Cyrtococcum accrescens* (Trin.) Stapf.	South East Asia
Poaceae	*Digitaria setigera* Roth	Pantropical
Poaceae	*Digitaria violascens* Link	Pantropical
Poaceae	*Eleusine indica* (L.) Gaertn.	Pantropical
Poaceae	*Imperata cylindrica* (L.) P. Beauv.	Pantropical
Poaceae	*Oplismenus compositus* (L.) P. Beauv.	Asia, Malay

Poaceae	*Paspalum conjugatum* P. J. Bergius	Asia, Malay
Poaceae	*Urochloa glumaris* (Trin.) Veldkamp	South East Asia
Polypodiaceae	*Microsorum scolopendria* (Burm. F.) Copel.	Pantropical
Rubiaceae	*Borreria laevis* (Lam.) Griseb.	America, Asia
Rubiaceae	*Rubiaceae* sp. I	
Schizaeaceae	*Lygodium circinnatum* (Burm.) Sw.	Asia, Malay
Schizaeaceae	*Lygodium microphyllum* (Cav.) R.Br.	Africa, Asia
Selaginellaceae	*Selaginella caudata* (Desv.) Spring	Indonesia
Selaginellaceae	*Selaginella willdenovii* (Desv.) Baker	Asia, Malay
Solanaceae	*Solanum torvum* Sw.	Pantropical
Taccaceae	*Tacca palmata* Blume	Indonesia
Thelypteridaceae	*Christella parasitica* (L.) Holttum.	Pantropical
Urticaceae	*Elatostema retinervium* Perrya	Indonesia
Urticaceae	*Urtica* sp. I	
Zingiberaceae	*Zingiberaceae* sp. I	

TABLE S2. List of all herb species recorded in the study with indication of their biogeographical distributions.

Responses of terrestrial herb assemblages to weeding and fertilization in cacao agroforests in Indonesia

Daniele Cicuzza[1], Yann Clough[2], Sri Sudarmiyati Tjitrosoedirdjo[3] and Michael Kessler[1]

[1]*Institute of Systematic Botany, University of Zurich, Switzerland.*
[2]*Agroecology, University of Göttingen, Germany.*
[3]*Department of Biology, Bogor Agricultural University, Indonesia.*

Submitted to: *Agroforestry System*

ABSTRACT

Terrestrial herbs are important ecological components in tropical agroforests, but little is known about how agricultural management affects herb communities. In cacao agroforests of Central Sulawesi, Indonesia, we studied the change in herb species richness, cover, and biomass over three years in 86 subplots subjected to high and low weeding frequency as well as fertilized and non-fertilized treatments. We recorded 111 species with a rapid change in species composition among the three years. Species richness increased sharply in the 2nd year, presumably as a result of the change in the management with the onset of the experimental regimes, and decreased in the 3rd, probably due to competitive exclusion. Species richness, cover, and biomass were all significantly higher in the infrequently weeded plots than in the frequently weeded ones, but there were only slight responses to the fertilization treatment. Although an indicator species analysis recovered 45 species that were typical for a given year and a further eight that were typical for certain treatments, these species showed no clear patterns relative to their ecology or biogeography. We conclude that the herb assemblages in cacao agroforests are quite resilient against weeding, but that the cover of individual species shifts rapidly in response to changes in management.

Key words: weed management, Cacao, agroforests, Sulawesi.

INTRODUCTION

Tropical agroforests, in which mostly coffee and cacao are cultivated under a canopy of shade trees, cover approximately 18 million hectares worldwide and are of oustanding economic and ecological importance (Donald 2004). Agroforests typically harbour a high level of biodiversity (Bhagwat et al. 2008), including a large number of terrestrial herbaceous plants (Steffan-Dewenter et al. 2007). Because herbs compete with the crop species for light, water, and nutrients especially when trees are young, and can also harbour diseases and pests, farmers commonly control herb populations by manual weeding or by applying herbicides (Aguilar at al. 2001). On the other hand, herbs can be important host plants for insect pollinators or natural antagonists of agricultural pests and diseases (Bos et al. 2007, Perfecto & Snelling 1995, Philpott & Armbrecht 2006). For example, flowering plants are important to maintain high bee species richness and result in a better pollination in coffee plantations (Klein et al. 2003). Herbaceous plants have often been neglected in biodiversity inventries of cacao and coffee plantations, with studies most often focussing on trees, insects and vertebrates (Bisseleua et al. 2008, Philott et al. 2008, Tscharntke et al. 2008, Abrahamczyk et al. 2008, Greenberg et al. 2000, Faria & Baumgarten 2007, Weist et al. 2010).

Management practices affect the composition and diversity of herb assemblages. The density and composition of the shade tree canopy varies strongly between agroforests, which range from rustic systems established under the thinned canopy of natural shade trees to technified systems completely lacking shade trees. The density and diversity of terrestrial herbs typically increases in plantations with a more open canopy which allows more light to reach the ground (Zapfack et al. 2002). However, many of the species found in sunny plantations commonly are weedy,

pantropical species (Zapfack et al. 2002) whereas more densely shaded plantations generally harbour species more typically found in forests (Bobo et al. 2006) and often with more restricted ranges (Lozada et al. 2007). As such, the latter assemblages are of higher conservation concern (Cicuzza et al. 2010).

In the scope of an interdisciplinary project addressing ecological and socioeconomic aspects of Indonesian cacao agroforests (Clough et al. 2010), over two years we studied how management practices influence the diversity and composition of the terrestrial herb assemblages. We use the data to address questions regarding the impact of management in the cacao agroforests on herbaceous plant communities. We asked the following questions:

(i) Do species richness, cover, biomass, and composition of the terrestrial herb assemblages change over two years in relation to two management aspects (weeding, fertilization)?

(ii) Are particular species typical for specific management regimes?

(iii) Is there a relationship between the management regimes and the presence of native or weedy herb species?

Study area

The study was conducted between 400 m and 1000 m in the Kulawi and Palolo valleys, at the northern and the western borders, respectively, of Lore Lindu National Park, Central Sulawesi (Fig.1). The region has relatively constant temperatures, with monthly minimum temperatures between 12°C and 17°C, while maxima range from 26°C to 35°C. Mean annual precipitation is around 2000 mm, with no month receiving less than 100 mm on average; although in some years

monthly values can be far lower (The Nature Conservancy 2004). The natural vegetation is evergreen tropical forest (Cannon et al. 2007).

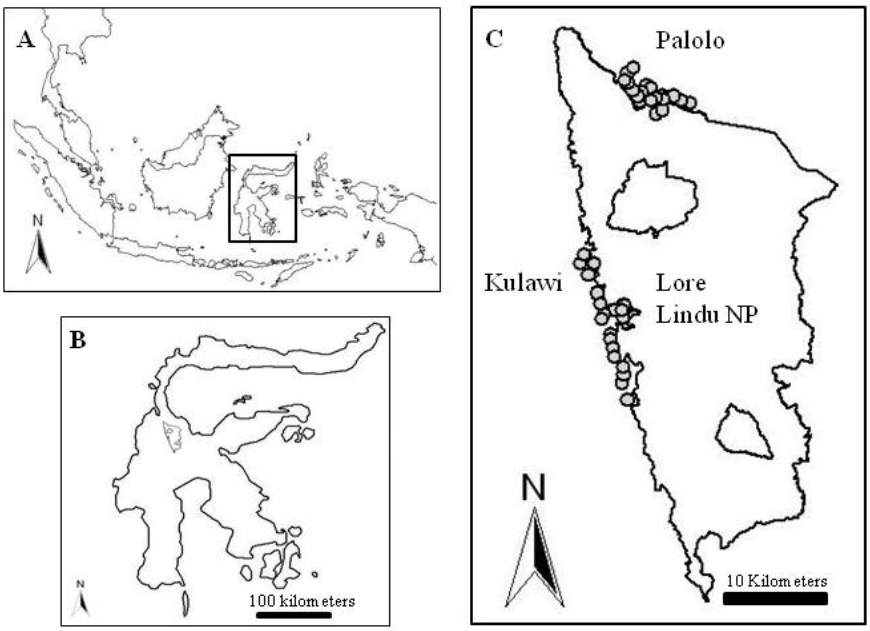


Fig.1. Maps of study area: (A) The Malay archipelago with the island of Sulawesi highlighted; (B) Sulawesi with the Lore Lindu National Park border; (C) Lore Lindu National Park with the position of the 43 research plots (circles) in Palolo and Kulawi valleys.

Beginning in the 80ies more than 7500 hectares of cacao plantations have been established in and around the national park (Erasmi et al. 2004). Plantations mostly have an open to dense canopy of shade trees, which are either remnant trees from the thinned native primary or old secondary forest (rustic cacao), polycultural stands of planted fruit or timber trees such as candlenut *Aleurites moluccana* (L.) Willd., rambutan *Nephelium lappaceum* L.,*Persea americana* Mill., langsat (longan) *Lansium domesticum* Correa, and durian *Durio zibethinus* Rumph. ex Murray (planted shade cacao), or species-poor stands of the leguminous trees *Gliricidia sepium* (Jacq) Kunth ex Walp. and *Erythrina subumbrans* (Hassk.) Merr. with a further management intensification to the complete removal of trees for full sun production (technified cacao) (Rice & Greenberg 2000, Kessler et al. 2005, Clough et al. 2009).

Vegetation sampling

Our study was part of a larger project aimed at elucidating the relationships of cacao management and yield as well as biodiversity (Steffan-Dewenter *et al.* 2007). For this, 43 plots, 22 in Kulawi and 21 in Palolo valley, of 40 m x 40m each, were rented from the local farmers from July 2006 to October 2008 and managed in a consistent way across all plots. The plots were treated differently before the beginning of our management experiment. Plantations were selected to cover the widest possible range of elevation, shade tree density and diversity, and distance from the natural forest (Clough et al. 2009). Plots selected were not treated with herbicides in the previous six month before the onset of the project. Twenty one plots were randomly assigned to a frequent manual weeding regime (every 2 months), the other twenty two to infrequent manual weeding (every 6 months). Each plot was further divided into two 20 m x

40 m subplots and one half fertilized twice a year with urea fertilizer (46% N) placing 217g urea (100g N) per cacao tree with aliquots placed into 10 holes around each tree, which were subsequently covered.

Field work for the present study was conducted during the months of September and October of 2006, 2007 and 2008. In 2006, we established in each plot two subplots of 8 m x 8 m each, one in the fertilized and the other in the non-fertilized half (Fig. 2). In the center of each subplot, we roped off an area of 5 m x 5 m which was not disturbed except for the management activities of the cacao plantation. This area was used to monitor the composition of the herb vegetation. In the peripheral area, we established 9 quadrates of 1 m x 1 m each. These were sampled destructively in each field season (2 in 2006, 3 each in 2007 and 4 in 2008) to measure above- and below-ground biomass.

To assess herb community composition, we recorded all terrestrial herb species and estimated their average height and total cover (in classes: 0-1%, 1-5%, 5-10%, 10-20%, 20-40%, 4-60%, 60-80%, 80-100%). Voucher specimens were collected for all species with at least seven duplicates and deposited in Herbarium Celebense, Palu (CEB), Herbarium Bogoriense, Bogor (BO), and the herbaria of Göttingen (GOET), Leiden (L), Zürich (Z), and UC Berkeley (UC, ferns only). Identifications were done at the herbaria of Göttingen (GOET) and Leiden (L); species difficult to determine were sent to specialists for identification.

Above and below-ground weed biomass was harvested in the 1x1m^2 plots within the area of each subplot (Fig. 2). The biomass collection was conducted only in the Kulawi valley. Samples were separated, dried and weighted by below- and above-ground components.

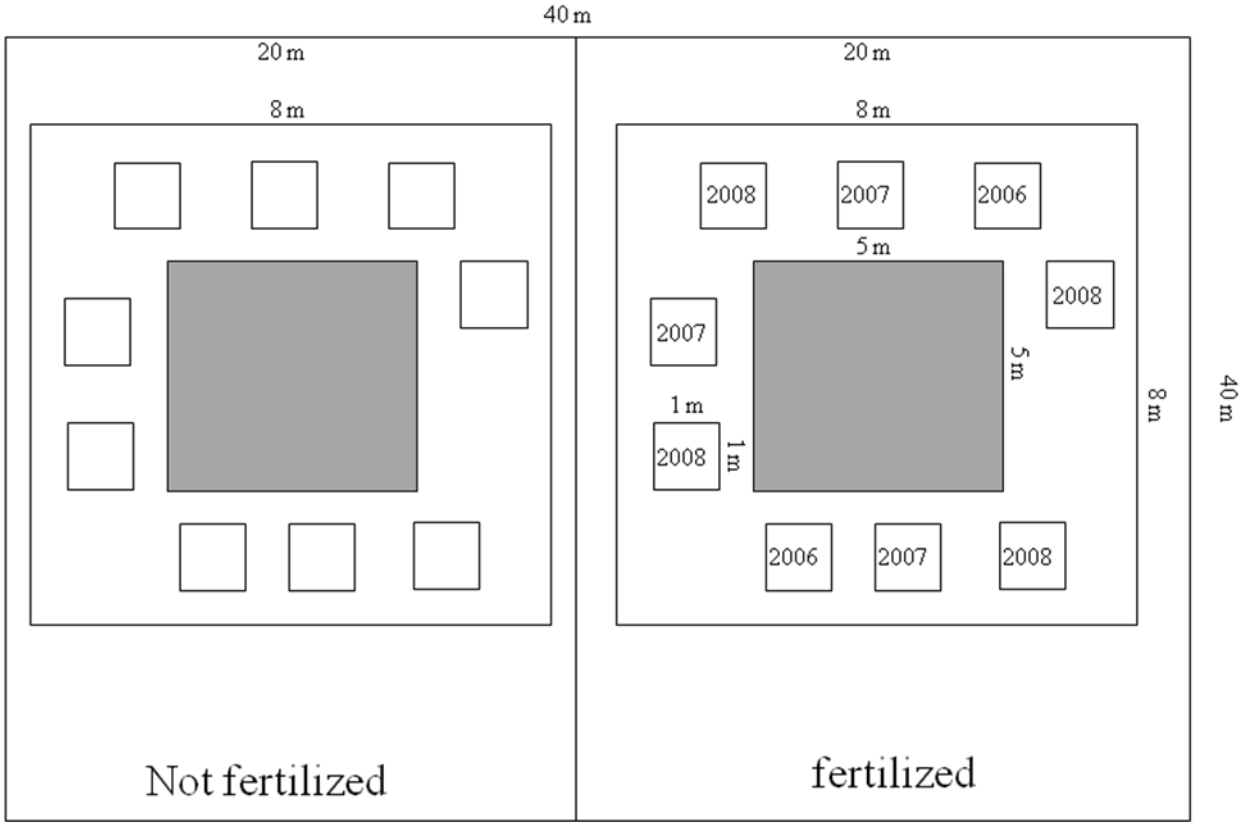


Fig. 2. Plot design; the overall plot of 40 x 40 m^2 was subdivided into two fertilization treatment subplots including in turn each a plot of 8 x 8 m^2 where our herb study was carried out. The 5 x 5 m^2 plot inside (grey) was used to monitor the herb assemblages. Biomass samples were taken in the 1 x 1 m^2 plots surrounding the monitoring area. Graph not to scale.

data analysis

To estimates sampling completeness, we used the program Estimates*S* v 8.2 (Colwell 2008), applying the mean of eight species richness estimators (ACE, ICE, CHAO2, JACK1, JACK2, BOOTSTRAP, MMMEAN, MMRUNS) (Herzog et al. 2002, Chiarucci et al. 2003).

To address changes in species richness, cover, and biomass in relation to the sampling years and to the management regimes, we performed repeated-measures ANOVAs separately for fertilization and weeding. To identify changes in species richness, cover and biomass we also used generalized linear mixed models (Bolker et al. 2009) obtaining quantitatively similar results to those of the repeated-measures ANOVAs. These results are not further shown here. To assess changes in species composition we used a Principal Component Analysis (PCA) based on the Bray-Curtis similarity index (Oksanen et al. 2007). Further, we used Analyses of Similarity (ANOSIM) to assess if shifts in species composition between years or between management regimes where significant. ANOSIM is a non-parametric permutation test that is analogous to an ANOVA for similarity matrices (Clarke et al. 2008). Finally, we used Indicator Species Analyses (Bakker 2008, Mouillot et al. 2002) to determine which species were characteristic for different years or management regimes. Indicator species were classified as typically growing in forests or in open habitats as well as being pantropical or having a geographical distribution restricted to Malayan archipelago based on personal field and herbarium experience (Cicuzza et al. 2010) and information from the literature. Analyses were performed in R (R Development Core Team 2007), with an additional function provided by R package vegan (Oksanen et al. 2007). Indicator species analysis was conducted with PCOrd 5.0 (McCune et al. 1999).

RESULTS

Species richness, cover, and biomass

During the three years, we recorded 111 herbs species. The mean of the eight species richness estimators was 120±6, indicating that our 43 study plots included most (about 90%) of the herb species occurring in cacao plantations in the study region.

Comparing the years, 56 species were recorded in 2006, 90 in 2007, and 72 in 2008; 32 species were recorded in all three years, but there was also strong turnover in species composition, with 13 species recorded only in 2006, 17 in 2007 and 10 in 2008 (Fig. 3).

Species richness was significantly different between weeding treatments but not between fertilization treatments (Tab. 1). In 2007 and 2008, weeded plots had significantly fewer species than non-weeded plots (Fig. 4). Herb cover per subplot varied from 0% to 100%. Comparing the years, cover increased significantly over the years (Tab. 1, Fig. 4). Cover changed significantly in the weeding treatment but not in the fertilization treatment (Tab. 1). In 2007 and 2008, weeded plots had significantly lower cover than non-weeded plots (Fig. 4). Fertilization had a small positive effect increasing the above ground biomass; the effect was more pronounced in the weeding treatment and also differed between years in the weeding treatment (Tab.1, Fig. 4). Below- and above-ground biomass increase in both of the treatments: weeding and fertilizing the cacao plantation showed a positive and significant increase in biomass, differing between the years of treatment.

	Species richness		Cover		Above-ground biomass		Below-ground biomass	
	F	P	F	P	F	P	F	P
Fertilized treatment								
Years	48.9	0.00	21.96	0.00	4.22	0.17	7.69	0.00
Fertilization	0.03	0.85	1.20	0.27	4.04	0.05	2.70	0.10
Years-Fertilization, interaction	0.11	0.90	0.66	0.52	0.09	0.92	0.09	0.91
Weeding treatment								
Years	48.2	0.00	22.92	0.00	5.00	0.01	9.92	0.00
Weeding	17.14	0.00	0.64	0.46	21.06	0.00	26.26	0.00
Years-Weeding, interaction	2.29	0.10	4.61	0.01	1.25	0.29	4.19	0.17

Tab. 1. Repeated-measures ANOVAs comparing mean values of species richness, ground cover, above- and below-ground biomass between years for two different experimental treatments (fertilization; weeding intensity).

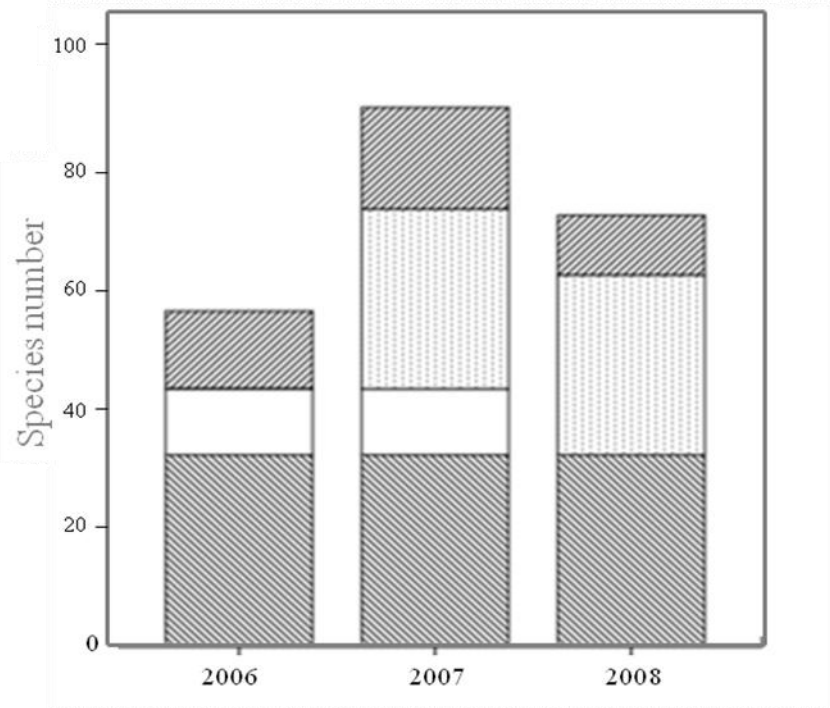


Fig. 3. Total number of herb species recorded in the three years in our study plots. Lower cross-hatched area: species recorded in all years; white area: species only recorded in both 2006 and 2007; dots: species only recorded in both 2007 and 2008; upper cross-hatched area: species only recorded in a given year.

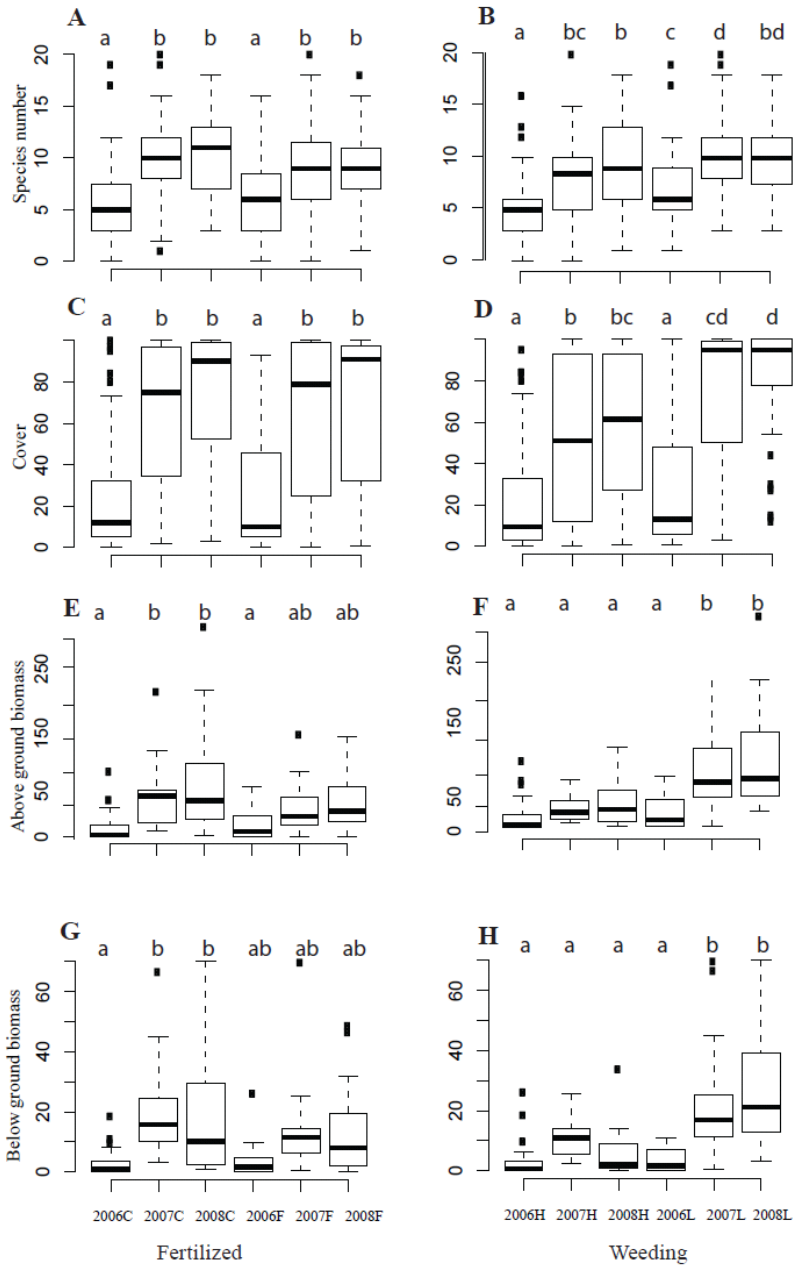


Fig. 4. Changes in traits of herb assemblages under different management regimes over two years of study. Box plots show mean (bold line), the 25th and 75th percentile (box), 95% of confidence interval (whiskers), and outliers (dots). Categories with different superscript letters are significantly different from each other (Tukey's HSD). C = control, F = fertilized, H = high weeding frequency; L = low weeding frequency.

Species composition

Species composition of the plots shifted significantly over the years (ANOSIM: R= 0.24, P=0.01), although this trend was mainly driven by a few plots, while the majority of plots only showed marginal changes (Fig. 5). An associated Indicator Species Analysis found that no fewer than 45 species had significantly higher cover in a given year: 8 species in 2006, 15 in 2007, and 22 in 2007 (Tab. 2). However, we found no significant differences in the frequency of forest-based versus open-country species (G-test, G=1.44, P >0.05) nor between pantropical and regional species (G-test, G=0.93, P >0.05).

Considering the experimental treatments, we found marginally significant shifts in species composition relative to weeding (ANOSIM, R=0.018, P= 0.06) but not relative to fertilization (R=-0.04, P=0.90). The indicator species analysis found five species with significantly higher frequency in plots weeded only every six months, three species typical for frequently weeded plots, and 2 species for plots that were fertilized (Tab. 3).

2006	2007	2008
	Axonopus compressus	
Bidens pilosa L. ** $$	(Sw.) P. Beauv. * $$	*Adenostemma lavenia* (L.) Kuntze
Commelina difformis L.	*Borreria laevis* (Lam.)	
** $	Griseb ** $$	*Aracea* sp
Costus speciosus (J.	*Christella parassitica*	
König) Sm. ** $	(L.) Holttum ** $	*Asplenium nidus* L.* $$
Emilia sonchifolia (L.)	*Cyrtococcum accrescens*	
DC.** $	(Trin.) Stapf. * $	*Asteraceae* sp.
	Crassocephalus	
Impatient platypetala ssp.	*crepidioides* (Beth.) S.	
Platypetala * $	Moore ** $$	*Begonia* * $
Pogonatherum crinitum	*Cyathula prostrata* (L.)	
(Thunb.) Steud.	Blume ** $$	*Borreria* sp.
Schismatoglottis dorensis	*Cynedrella nodiflora*	
Gibbs * $	(L.) Gaertn. ** $$	*Centella asiatica* (L.) Urb. ** $$
Sphaerostephanos invisus	*Elatostema parvum*	
(G.Forst.) Holttum ** $$	(Blume) Miq * $	*Centotheca lappacea* (L.) Desv. * $$
	Hygrophila sp.	*Commelina* sp. *
	Impatient platipetala	
	Lindl. * $	*Commelina benghalensis* L.** $$
	Impatient platipetala	*Convulvulacae* sp.

	var. Aurantica * $	
	Passiflora foetida L.** $$	*Curculigo latifolia* Dryand ** $$
	Trichosanthes trifolia (L.) Merr. * $	*Diplazium asperum* Blume** $
	Urochloa glumaris (Trin.) Veldk. * $	*Diplazium esculentum* (Retz.) Sw.** $$
		Elephantopus scaber L.** $$
		Impatient radicata Zoll.* $
		Labiata sp.
		Nephrolepis biserrata (Sw.) Schott * $
		Nephrolepis falciformis J. Sm.* $
		Paspalum conjugatum P. J. Bergium ** $
		Selaginella caudata (Desv.) Spring * $

Tab. 2. Results of the Indicator Species Analysis for the three years of treatment in cacao agroforestry systems. * species typically found in forest habitats, ** species typically found in non-forest habitats; $ species with distribution restricted to the Malay region, $$ pantropical species.

Low weed treatment	High Weed treatment	Fertilized
Microsorum scolopendria (Burm. F.) Copel. (1)	*Bidens pilosa* L. (2)	*Diplazium esculentum* (Retz.) Sw. (3)
Alocasia balgooyi A. Hay (2)	*Cyathula prostrata* (L.) Blume (3)	*Elatostema parvum* (Blume) Miq (3)
Borreria sp. (3)	*Adenostemma lavenia* (L.) Kuntze (3)	-
Cyrtococcum accrescens (Trin.) Stapf. (3)	-	-
Lygodium circinnatum (Burm.) Sw. (3)	-	-

Tab. 3. Results of the Indicator Species Analysis for the different treatments. The non-fertilized plots had no indicator species. Numbers indicate in which year the species were significantly more abundant: 1 = 2006, 2 = 2007, 3 = 2008.

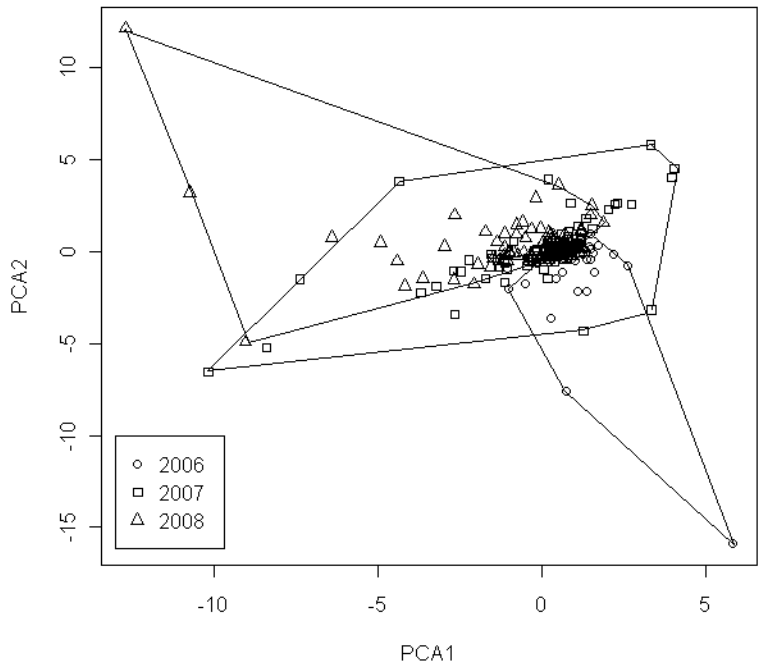


Fig. 5. Principal component analysis (PCA) of study plots based on the species abundance over the three years of study. Its shows a shift in species composition from the first to the third year of the study.

DISCUSSION

Overall, the results of our study can be summarized as follows: species richness, cover, biomass, and community composition all changed markedly between years and to a lesser degree between plots with frequent versus infrequent weeding, and with a minor effect for the fertilization treatments.

The change over the years can most likely be explained by the changes in management techniques in our experiment relative to the management conducted by the local farmers. In particular, farmers commonly use chemical herbicides to combat herbs. The increase in cover and species numbers between 2006 and 2007 was thus mainly the consequence of the change in management resulting from the onset of the experimental management treatments. Since most of the species newly recorded in 2007 are perennial rhizomatous herbs that were found as mature individuals, we assume that most of them were already present at the onset of the experiment but were simply not visible during sampling due to the previous weeding, including use of herbicides. Only two annual Asteraceae species, *Bidens pilosa* L. and *Crassochepalum crepidioides* (Benth.) Moore, played an important role in the herb assemblages, but only the latter increased in the course of the experiment while the first decreased. Thus, much of the increase of species numbers between the first two years may best be explained by the full aboveground development of plants that were already there.

The changes between the second and the three years in turn may reflect the competitive exclusion of some species by weedy species that, under reduced weed management intensity, could reach high cover and dominate the assemblages. Continued low weeding intensity could

thus reduce the vitality of some herbaceous species leading to decrease the total species diversity.

Although fertilization is well known to affect the composition of terrestrial herb assemblages (Efthimiadou et al. 2009), in our experiment we observed a small, but not statistically significant, increase of species number. The effect of fertilization was observed for both above- and below-ground biomass.

Single herbaceous species showed a particular increase on their frequency in the last year of fertilization. The fern *Diplazium esculentum* (Retz.) Sw. and the Urticaceae *Elatostema parvum* (Blume) Miq. Both increased significantly in the fertilized plots. Both of these are typically found in damp, nutrient-rich habitats such as road culverts and may thus be expected to respond positively to fertilization. Overall, the positive trend of increasing species number is not statistically significant, probably due to the short period of study.

Contrary to our expectations, we did not find any directional shifts in the frequency of light- versus shade-loving or widespread versus Malesian species over the course of the experiment. Possibly, these aspects are more closely linked to the density of the natural forest trees in the cacao plantation, and the distance to the natural forest, as previously documented in the study region (Steffan-Dewenter et al. 2007, Cicuzza et al. 2010), rather than to management practices.

In conclusion, we found that the herb assemblages in the studied cacao agroforests were strongly influenced by chemical and mechanical weeding but only slightly by fertilization. While these observations may appear to be trivial, their ecological implications may be far-reaching. A better developed herb layer may affect the diversity and community composition of amphibians and reptiles (Wanger et al. 2009) and insects (Wielgoss et al. 2010). Frequent weeding is well known to favour herb species with a certain suite of ecological characters, especially short reproductive

cycles and vegetative growth close to the ground (Aguillar et al. 2003). The shifts in species composition between the weeding treatments may thus also affect the physiognomy and phenology of the herb assemblages, again with implications for the associated biota. Herbs may also affect the water balance, litter decomposition, and nutrient cycling of the upper soil layer (Watanabe et al. 2007, Smiley & Kroschel 2010). Ultimately, these factors all influence the ecological and economical value of agroforests.

ACKNOWLEDGEMENTS

This study was funded by the German Research Foundation (DFG), grant SFB-552 STORMA (Stability of Rainforest Margins) http://www.uni-goettingen.de/de/40515.html. Herb species identification was conducted partly at the Herbarium of Leiden supported by Synthesys NL-TAF 3536. We thank to Stefan Köhler, head of the laboratory at Tadulako University. We thank Adam Malik, Wolfram Lorenz, Surya Tarigan, Muhammad Sigit and all plantation owners for their help in this work.

REFERENCES

Abrahamczyk S, Kessler M, Putra D, Waltert M, Tscharntke T (2008) The value of differently managed cacao plantations for forest birds conservation in Sulawesi, Indonesia. *Bird Conservation International* 18: 349-362.

Aguillar V, Staver C, Milberg P, (2003) Weed vegetation response to chemical and manual selective ground cover management in a shaded coffee plantation. Weed research 43: 68-75.

Bakker JD (2008) Increasing the utility of Indicator Species Analysis. *J. Appl. Ecol.* 45: 1829-1835.

Bhagwat SA, Willis KJ, Birks HJB, Whittaker RJ (2008) Agroforestry: a refuge for tropical biodiversity? *Trends Ecol Evolut* 5: 261-267.

Bisseleua D, Herve B, Vidal S (2008) Plant biodiversity and vegetation structure in traditional cocoa forest gardens in southern Cameroon under different management. *Biodiv. Conserv.*17:1821-1835.

Bobo KS, Waltert M, Sainge NM, Njokagbor J, Fermon H, Mühlenberg M (2006) From forest to farmland: species richness patterns of trees and understory plants along a gradient of forest conversion in Southwestern Cameroon. *Biodivers. Conserv.* 15: 4097-4117.

Bloker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evolut.* 24: 127-135.

Bos MM, Dewenter IS, Tscharntke T (2007) The contribution of cacao agroforests to the conservation of lower canopy ant and beetle diversity in Indonesia. *Biodivers. Conserv.* 16: 2429-2444.

Cannon CH, Summers M, Harting JR, Kessler PJA (2007) Developing conservation Priorities Based on Forest Type, Condition, and Threats in a Poorly Known Ecoregion: Sulawesi, Indonesia. *Biotropica*. 39: 747-759.

Cicuzza D, Kessler M, Clough Y, Pitopang R, Leitne D, Tjitrosoedirdjo SS (2010) Conservation value of cacao agroforests for terrestrial herbaceous plants in Central Sulawesi, Indonesia. *Biotropica*. Submitted (in press).

Chiarucci A, Enright NJ, Perry GLW, Miller BP, Lamont BB (2003) Performance of nonparametric species richness estimators in high diversity plant community. *Divers. Distribut*. 9: 283-295.

Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypothesis in explanatory community analyses: similarity profile and biota-environment linkage. *J. exp. mar. boil. ecol.* 366: 56-69.

Clough Y, Putra DD, Pitopang R, Tscharntke T (2009) Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry. *Biol. Conserv*. 142: 1032-1041.

Clough Y, Abrahamczyk A, Adams MO, Anshary A, Ariyanti N, Betz L, Buchori D, Cicuzza D, Darras K, Putra DD, Fiala B, Gradstein SR, Kessler M, Klein AA, Pitopang R, Sahari B, Scherber C, Schultze CH, Shahabuddin, Sporn S, Stenchly K, Tjitrosoerdjo SS, Wanger TC, Weist M, Wielgoss W, Tscharntke T (2010). Biodiversity patterns and trophic interactions in human-dominated tropical landscapes in Sulawesi (Indonesia): plants, arthropods and vertebrates. In T. Tscharntke et al. (ed.) Tropical rainforests and agroforests under global change, pp. 15-72. Springer, Berlin.

Colwell RK (2008) EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.0.0 User's guide and application. Available at: http://purl.oclc.org/estimates

Donald PF (2004) Biodiversity impacts of some agricultural commodity production systems. *Conserv. Biol.* 18:17-37.

Efthimiadou AP, Anestis C, Dimitrios BJ, Efthimiadis P (2009) The phenomenon of crop-weed competition; a problem or a key for sustainable weed management? *J. food agric. environ* 7: 861-868.

Erasmi S, Twele A, Ardiansyah M, Malik A, Kappas SM (2004) Mapping deforestation and land cover conversion at the rainforest margin in Central Sulawesi, Indonesia. *EARSeL e Prooceedings*. 3: 388-397.

Faria D, Baumgarten J (2007) Shade cacao plantations (*Theobroma cacao*) and bat conservation in southern Bahia, Brazil. *Biodiv. Conserv.* 16: 291-312.

Greenberg R, Bichier P, Angón AC (2000) The conservation value for birds of cacao plantations with diverse planted shade in Tabasco, Mexico. *Anim. conserv.* 3:105-112.

Herzog SK, Kessler M, Cahill TM (2002) Estimating species richness of tropical bird communities from rapid assessment data. *Auk* 119: 749-769.

Kessler M, Kessler PJA, Gradstein SR, Bach K, Schmull M, Pitopang R (2005) Tree diversity in primary forest and different land use systems in Central Sulawesi, Indonesia. *Biodiv. Conserv.* 14: 547-560.

Klein AM, Dewenter IS, Tscharntke T (2003) Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. London B.* 270: 955-961.

Lozada T, Koning de GHJ, Kessler M, Klein AM, Tscharntke T (2008) Geographical range size of tropical plants influences their response to anthropogenic activities. *Div. Distrib.* 14: 59-68.

Mc Cune Mefford (1999) PC-ORD Multivariate analysis of ecological data. Version 5. MjM Software Design, Gleneden Beach OR

Mouillon D, Culioli JM, Chi TD (2002) Indicator species analysis as a test of non-random distribution of species in the context of marine protected areas. *Envir.Conserv.* 29:385-390.

Oksanen J, Kindt R, Legendre P, O'Hara B, Stevens MHH (2007)Vegan:
Community Ecology Package. R package version 1.8-8 http://r-forge.rproject.org/project/vegan/.

Perfecto I, Snelling R (1995) Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. *Ecol. Appl.* 5:1084-1097.

Philpott SM, Armbrecht I (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecol. Entomol.* 31:369-377.

Philpott SM, Arendt WJ, Armbrecht I, Bichier P, Diestch TV, Gordon C, Greenberg R, Perfecto I, Reynoso-Santos R, Soto-Pinto L, Tejeda-Cruz C, Williams-Lenera G, Valenzuela J, Zolotoff JM (2008) Biodiversity loss in Latin American coffee landscape: review of the evidence on ants, birds and trees. *Conserv. Biodiv.* 22:1093-1105.

R development core team. (2007) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>

Rice RA, Greenberg R (2000) Cacao cultivation and the conservation of biological diversity. *Ambio* 29: 167-173.

Smiley SL, Kroschel J (2010) Yield development and nutrient dynamics in cocoa-gliricidia agroforests of Central Sulawesi, Indonesia. *Agroforest Syst*. 78:97-114.

Steffan-Dewenter I, Kessler M, Barkmann J, Bos MM, Buchori D, Erasmi S, Faust H, Gerold G, Glenk K, Gradstein RS, Guhardja E, Harteveld M, Hertel D, Höhn P, Kappas M, Köhler S, Leuschner C, Maertens M, Marggraf R, Migge-Kleian S, Mogea J, Pitopang R, Schafer M, Schwarze S, Sporn SG, Steingrebe A, Tjitrosoedirdjo SS, Tjitrosoedirdjo S, Twele A, Weber R, Woltmann L, Zeller M, Tscharntke T (2007) Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proc. Natl. Acad. Sci.* USA 12: 4973-4978.

The Nature Conservation (2004) Lore Lindu National Park Management Plan 2004-2029.
Entwistle PF (1972) Pest of Cocoa. First ed. Longman, London, UK.

Tscharntke T, Sekercioglu CH, Dietsch TV, Sodhi NS, Hoehn P, Tylianakis JM (2008) Landscape constraints of functional diversity of birds and insects in tropical agroecosystems. *Ecology* 89: 944-951.

Watanabe A, Takada Sarno H, Afandi, Adachi T, Oki Y, Senge M (2007) Assessment of degradation and generation of humus in a coffee soil affected by weed cover by means of a stable carbon isotopic ratio. *European Journal of Soil Science* 58:1042-1049.

Wanger TC, Saro A, Iskandar DT, Brook BW, Sodhi NS, Clough Y, Tscharntke T (2009) Conservation value of cacao agroforestry for amphibians and reptiles in
Southeast Asia: combining correlative models with follow-up field experiments. *J. Appl. Ecol*. 46: 823-832.

Weist M, Tscharntke T, Sinaga HM, Maryanto I, Clough Y (2010) Effect of distance to forest and habitat characteristics on endemic versus introduced rat species in agroforest landscapes of Central Sulawesi, Indonesia. *Mammalian Biology* In press.

Wielgoss A, Tscharntke T, Bucheri D, Fiala B, Clough Y (2010)Temperature and a dominant dolichoderine and species affect and diversity in Indonesian cacao plantations. Agricolture *Ecosystems and Environment* 135: 253-259.

Zapfack L, Engwald S, Sonke B, Achoundong G, Madong BA (2002) The impact of land conversion on plant biodiversity in the forest zone of Cameroon. *Biodiv. Conserv*. 11: 2047-2061.

Terrestrial herb communities of tropical submountane and tropical mountane forests in Central Sulawesi, Indonesia

Daniele Cicuzza[1,2], Michael Kessler[1,2] Ramadhanil Pitopang[3], Sri S. Tjitrosoedirdjo[4] and S. Robbert Gradstein[1]

[1] *Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany.*
[2] *Institute of Systematic Botany, University of Zürich, Zollikerstrasse 107, 8008 Zürich, Switzerland.*
[3] *Department of Forest Managment and Herbarium Celebense, Tadulako University, Palu, Indonesia*
[4] *Department of Biology, Faculty of Mathematics and Science, Bogor Agricultural University, Bogor, Indonesia*

Published in: Tropical rainforests and agroforests under global change. Teja Tscharntke, C. Leuschner, E. Veldkamp, H. Faust, E. Guhardja and A. Bidin (Eds.) Springer Berlin.

ABSTRACT

Although the diversity of terrestrial herbs is high tropical forests and although herbs may play important roles, e.g., as competitors of tree seedlings, most tropical botanical research to date has focused on trees. We studied the diversity, taxonomic composition, and biogeographical relationships of terrestrial forest herbs at two sites of tropical mountain forest at different elevations (Pono: 1000 m, Bariri: 1400 m) in Central Sulawesi. The study was conducted in 400 plots of 5 x 5 m^2 (200 for each site). At Pono, we recorded 91 angiosperm herb species in 28 families, and 112 ferns and lycophytes in 15 families whereas at Bariri we found 77 angiosperms in 25 families and 94 ferns and lycophytes in 20 families. At both sites, the most species-rich angiosperm families were Araceae, Orchidaceae, and Zingiberaceae. The species numbers recorded by us are much higher than those reported in any previous tropical forest herb inventories and point to a previously underappreciated richness of plant assemblages on Sulawesi. Biogeographically, significantly more fern species reached their western than eastern distributional limits on Sulawesi, showing that the zoogeographical Wallace's line separating continental Asia and its shelf islands from the Moluccan region also holds for spore-dispersed plants.

Keywords: herbs diversity, species richness, Indonesia, Sulawesi, tropical mountain forest

INTRODUCTION

Tropical forests contain the most species-rich plant communities (Jacobs 1988) and the Malasian region is considered among the most diverse worldwide with over 40,000 vascular plants species (Baas et al. 1990; Roos 1993). Sulawesi, the largest island of the Wallacean region located between the Greater Sunda Islands and New Guinea, is generally considered to have intermediate levels of plants species richness (Roos et al. 2004). This can be explained by several factors. First, among the larger Indonesian islands, Sulawesi has the lowest collection rates, with less than 25 collections per 100 km^2, and taxonomic studies have been limited (Cannon et al. 2007). Second, historical isolation from the Sunda Shelf through the Quaternary Period prevented the continental enrichment experienced by Borneo, Sumatra, and Java (Whitmore 1987, Hall and Holloway 1998, Moss *et al.* 1998). Third, Sulawesi has a peculiar geography with four narrow peninsulas radiating from a small central area, so that no location is more than 100 km from the coast, resulting in a unique large island without inland (Cannon et al. 2007). On the other hand, Sulawesi has a complex geology, and the long isolation has allowed the evolution of a characteristic and unique flora and fauna, resulting in some of the highest levels of endemisms in the region (Roos et al. 2004; Cannon et al. 2007).

Most studies on tropical vegetation ecology have focused on trees at the expense of herbs, even though the latter may be a major component of the biodiversity of these forests (Poulsen & Pendry 1995). Herbs may be important competitors of tree seedlings and can thereby impact the diversity and composition of the tree communities. Also, due to their rapid life cycle, they may react rapidly to environmental changes, but to date there are no studies concerning understory herb species as possible indicators of reactions of tropical plant communities to

global change. Among the few studies inventoring terrestrial herbs in tropical forests, Poulsen & Pendry (1995) for example found 121 species corresponding to 85 angiosperms and 36 ferns at Bukit Belalong, Brunei, Borneo. In South America, Poulsen et al. (2006) found 123 species (29 ferns, 24 palms, and 70 other angiosperms) in Peru, whereas in Amazonian Brazil, Costa (2004) recorded 35 herb species (11 ferns, 24 angiosperms). These and other studies document a wide range of variation in species richness and taxonomic composition of tropical herb communities that is not yet fully understood. To date, there are no specific studies of forest herbs on Sulawesi (Cannon 2001). In the present study, we therefore present the first inventories of terrestrial forest herbs at two tropical mountain forest sites in Lore Lindu National Park, Central Sulawesi. To study biogeographical affinities of the terrestrial herb assemblages, we focused on the pteridophytes.

MATERIAL AND METHODS

Study sites and field sampling

Lore Lindu National Park is one of the largest and most important conservation areas in Sulawesi, containing a unique range of habitats (Cannon 2001). Our study was conducted at two localities within the park (Fig. 1). The Bariri site was located in old-growth montane forest at about 1430 m elevation on the eastern side of the Lore Lindu National Park, near Bariri village, province of Poso (1º39’28.44 S 120º10’24.6 E). The Pono site was located in submontane forest at about 1000 m near the western side of the National Park, just east of Toro village (1º 30’ 35.383S 120º 3’ 25.169E). Human impact on both sites is slight and limited to hunting and gathering of some forest products, especially rattan.

At both study sites, we established a network of 200 non-permanent plots of 5 x 5 m^2 each, over an area of about 0.7 km^2 (Fig. 1). Distance between adjacent plots was 20 m for all plots at Pono, whereas at Bariri 120 plots were 20 m apart and the remaining 50 m. Plot layout at each locality was designed to representatively cover the range of topographical conditions (ridges, slopes, valley bottoms) within a given elevational range. Field work was conducted in February 2007 at Bariri and in December-February 2008 at Pono. In each plot, all species of herbs were sampled semiquantitatively recording cover in classes (0-1%, 1-5%, 5-10%, 10-20%, 20-40%, 40-60%, 60-80%, 80-100%). Juvenile individuals less than 10 cm tall and difficult to identify were not recorded.

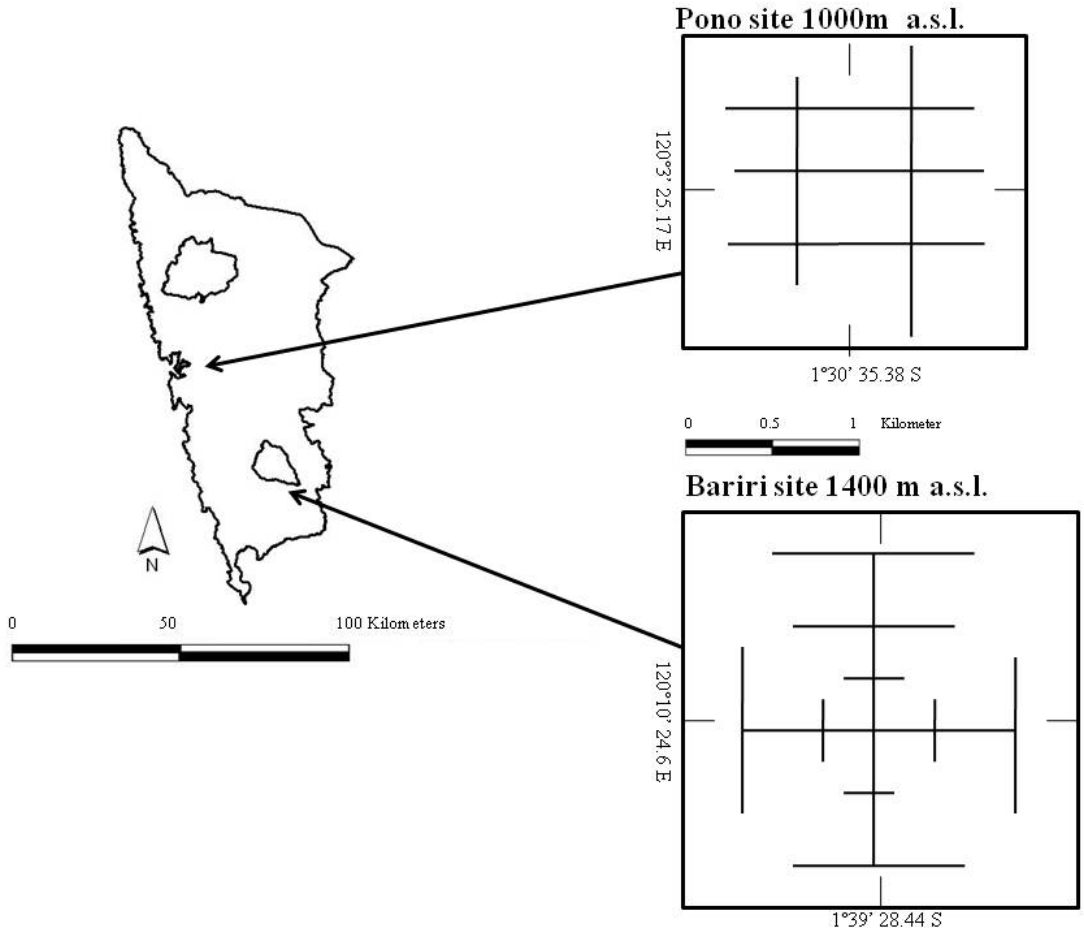


Figure 1. The outline of Lore Lindu National Park in Central Sulawesi, showing the general location of the two study sites, and details of the plot layout at the two sites, with the individual study plots placed along the transect lines.

Voucher specimens were collected for all species within a study area (not in every single plot) with at least seven duplicates. Identification of plant species was done at the herbaria of Göttingen (GOET) and Leiden (L); species difficult to determine were sent to specialists for identification. The collections were deposited in Herbarium Celebense, Palu (CEB), Herbarium Bogoriense, Bogor (BO), and the herbaria of Göttingen (GOET), Leiden (L), Zürich (Z), and Berkeley (UC, ferns only). Information on species distribution ranges was obtained from the Flora Malesiana Series (e.g., 1981, 1991, and 1998) and from the botanical database Tropicos (www.tropicos.org).

In each plot, we measured the following environmental variables: elevation, slope inclination, and relative topographical position divided in four categories (shoulder, backslope, footslope and depressional complex). Soil samples were collected in the center of each plot and analyzed for a wide range of parameters (Tab. 1).

	Pono	Bariri
Elevation mean (m)	1050	1422
Elevation minimum and maximum (m)	900-1100	1400-1500
Mean annual temperature (°C)	20.8	19.6
Mean annual precipitation (mm)	3534	1984
pH (mean, min, max)	3.85 (3.01-5.09)	3.91 (3.31-6.84)
C/N (mean, min, max) (of 200 plots)	12.8 (2.71-20.63)	12.73 (8.40-21.3)
C mean (min, max)	3.14 (0.49-7.37)	2.52 (0.70-5.68)
N mean (min, max)	0.25 (0.02-0.48)	0.19 (0.05-0.33)

Tab. 1. Environmental characteristics of the study sites. Means and ranges are based on the values of the 200 plots per site, except for climate variables that were measured at one station at each site.

RESULTS

At Pono, we recorded 91 angiosperm herb species in 28 families, and 112 ferns and lycophytes in 15 families, resulting in a total of 203 terrestrial herb species. Of these, 122 samples were identified to species level, 53 to genus level and the remaining 28 to family level. The most species-rich families were Araceae (20 spp.), Orchidaceae (16 spp.), and Zingiberaceae (10 spp.). Among the ferns and lycophytes, the Polypodiaceae had 15 species, followed by Aspleniaceae, Pteridaceae, and Woodsiaceae with 12 species each. At Bariri, we recorded a total of 171 terrestrial herb species, corresponding to 77 angiosperms in 25 families and 94 ferns and lycophytes in 20 families. At this site, 50 samples were identified to species level, 30 to genus, and 91 to family. The most species-rich angiosperm families were Zingiberaceae (16 spp.), Orchidaceae (13 spp.), and Araceae (10 spp.). Among ferns and lycophytes highest species richness was found in Polypodiaceae (16 spp.), Aspleniaceae (11 spp.), and Hymenophyllaceae (9 spp.). Species-accumulation curves for both sites showed signs of saturation, indicating that overall sampling was representative (Fig. 2). This impression was supported by an estimation of the total species richness with the Chao2 estimator (Herzog et al. 2002, Walther & Moore 2005), which predicted total species numbers of 223 for Pono and 221 for Bariri, suggesting that about 91% and 68%, respectively, of all herb species at the sites were encountered.

Terrestrial herbs were recorded in all individual plots, but species richness varied from 1-26 (mean 14.0) species per plot at Bariri and 2-28 (mean 9.7) species at Pono, whereas collective ground cover of all herbs in a plot ranged from 0.01-100 % per plot at Bariri and 0.05-100 % at Pono. These values were not significantly different between sites (t-tests, $P > 0.1$). Ferns and lycophytes were the dominant groups of terrestrial herbs both from the cover index and from the

species numbers. Their mean cover index was 48% at Pono and 79% at Bariri, compared to 26% and 7%, respectively, for angiosperms.

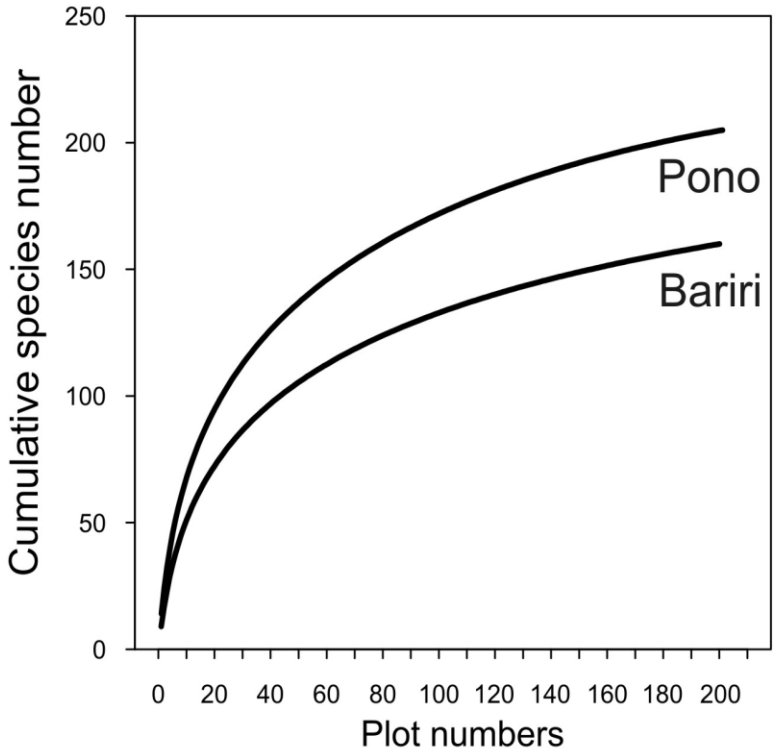


Figure 2. Species-area curves for the two study sites Pono and Bariri. To calculate the species-accumulation curves the order of the 200 study plots at each site was repeatedly randomize 50 times.

Because species-level identification was more complete and reliable for ferns and lycophytes (50%) than for angiosperms (23%) (frequently found only in sterile condition), subsequent biogeographical analyses were only based on ferns and lycophytes. At both sites most fern and lycophyte species had distribution ranges covering the entire Malesian Region and often extending to Indochina (Tab. 2). However, at Pono no fewer than 7 species (13%) are currently considered to be endemic to the island of Sulawesi, whereas no such species were recorded at Bariri. The number of geographically widespread species (tropical Asia to pantropical) was limited at both sites. At Bariri, 18 fern and lycophyte species reached their western distributional limits on Sulawesi and extended eastwards to the Moluccas, New Guinea or partly beyond. In contrast, only 4 species found at Bariri reached their eastern limits on Sulawesi. These numbers differed significantly from each other (Chi^2-test, $Chi^2 = 16.70$, $P < 0.01$). At Pono, there were also more species with western (9) than eastern (3) range limits, but this difference was not quite significant (Chi^2-test, $Chi^2 = 3.84$, $P < 0.10$)

Distribution	Pono	Bariri
Endemic to Sulawesi	7 (13)	0 (0)
Endemic to Malesia	14 (25)	27 (61)
Malesia + Indochina	19 (35)	15 (34)
Tropical Asia	6 (11)	0 (0)
Tropical Asia + Africa	3 (5)	1 (2)
Pantropical	6 (11)	2 (5)
Reaching W limit in Sulawesi	9 (16)	18 (40)
Reaching E limit in Sulawesi	3 (6)	4 (9)

Tab 2. Geographical distribution of the fern and lycophytes species recorded at Pono (55 species) and Bariri (44 species) based on herbarium and literature information. Values in parentheses are percentages.

DISCUSSION

The numbers of terrestrial herb species recorded at both of our study sites was higher than those of any other inventory in tropical forests conducted to date (Tab. 3). This may partly be due to the high number of sampled plots spread over an extensive area (0.7 km^2) in our study, but other studies also covered large areas and this alone can certainly not explain the striking difference relative to previous studies. Traditionally, based on the knowledge of animal groups such as snakes (Bosch 1985) and birds (White and Bruce 1986), biotic communities on Sulawesi have been considered to be only moderately rich in species but containing exceptional levels of endemism (Backer and Bakhuizen van den Brink 1963). Studies of plant species numbers across the Sundaic region placed Sulawesi in an average position between less diverse Java and Sumatra on the one hand and more species-rich New Guinea and Borneo on the other (Roos at al. 2004). The moderate diversity and high endemism of Sulawesi have been explained by the limited island size along with the long-term geographical isolation of the island, which has limited colonization and has allowed the evolution and persistence of numerous unique forms (Backer and Bakhuizen van den Brink 1963, Whitten et al. 1987, Roos at al. 2004). However, recent quantitative botanical data suggest that plant communities may be more species-rich on Sulawesi than generally thought. Tree inventories in Lore Lindu National Park show species numbers that are comparable to those of mainland Southeast Asia and the Philippines, or even higher (Schulze et al. 2004, Kessler et al. 2005). Similarly, fern communities on Sulawesi are richer than those on Java, Borneo, and in Peninsular Malaysia (M. Kessler and J. Kluge, unpubl. data), even though they do not approach species numbers from South America (Kessler 2001,

Kluge et al. 2006). Bryophyte species richness on Sulawesi is also among the highest ever reported for tropical forests (Sporn et al. 2009). Our study suggests that forest herbs on Sulawesi may also be unexpectedly diverse, although additional surveys from other sites on the islands as well as elsewhere in the tropics are needed to corroborate this impression. The discrepancy between the high diversity of these local studies and the moderate diversity reported based on general collecting activities may well be the low density of botanical collections on Sulawesi, with is less than 5% of that on Java, for example (Cannon 2001).

Locality	**Elavation (m)**	**Mean annual precipitation (mm)**	**Area (m^2)**	**Families**	**Genera**	**Species**	**Fern and lycophytes**
Pono, Sulawesi	1000	3534	5000	45	93	203	112 (55)
Bariri, Sulawesi	1400	1984	5000	42	80	171	94 (55)
Brunei, Borneo	800	5000	250	27	46	74	15 (20)
Brunei, Borneo	1000	5000	250	22	23	27	5 (19)
Brunei, Borneo	1100	5000	250	31	52	99	35 (35)
SW India	600-660	1600	1200	53	132	155	13 (10)
SW India	<900	1014	3200	32	39	42	3 (10)
SW India	900-1300	1014	3200	26	35	39	3 (12)
Budongo, Uganda	1200	1150-1500	2500	22	74	117	32 (27)
Bwindi, Uganda	1450	1400-1900	2500	21	70	101	42 (42)
Merida, Venezuela	2600	2500	400	13	17	20	14 (70)
Manaus, Brazil	80	2478	880	18	24	35	11 (31)
Cuyabano, Ecuador	250-300	---	1000	26	50	99	29 (29)

Los Volcanes, Bolivia deciduous	1050-1100	1200-1500	1000	4	26	31	7 (23)
Los Volcanes, Bolivia, semideciduous	900-1000	1200-1500	1000	6	28	47	17 (36)
Los Volcanes, Bolivia, evergreen	900-950	1200-1500	1000	8	33	63	25 (40)

Locality	Angiosperms	Araceae	Orchidaceae	Zingiberaceae	Other families	Reference
Pono, Sulawesi	91 (45)	20 (22)	16 (18)	10 (11)	45 (49)	This study
Bariri, Sulawesi	77 (45)	10 (13)	13 (17)	16 (21)	38 (49)	This study
Brunei, Borneo	59 (80)	10 (17)	7 (12)	20 (34)	22 (37)	Poulsen and Pendry (1995)
Brunei, Borneo	22 (81)	1 (4)	5 (23)	7 (32)	9 (40)	Poulsen and Pendry (1995)
Brunei, Borneo	64 (65)	10 (16)	4 (6)	21 (33)	29 (45)	Poulsen and Pendry (1995)
SW India	124 (90)	2 (2)	6 (4)	8 (6)	108 (79)	Annaselvan and Parthasarathy (1999)
SW India	28 (90)	2 (6)	0	0	26 (84)	Chittibabu and Parthasarathy (2000)
SW India	22 (88)	2 (8)	0	0	20 (80)	Chittibabu and Parthasarathy (2000)
Budongo, Uganda	85 (73)	4 (5)	13 (15)	10 (12)	58 (68)	Poulsen (1997)
Bwindi Uganda	59 (58)	2 (3)	8 (14)	6 (10)	43 (73)	Poulsen (1997)
Merida Venezuela	6 (30)	0 (0)	2 (33)	0 (0)	4 (67)	Kelly et al. (1994)
Manaus, Brazil	24 (69)	2 (8)	0 (0)	1 (4)	21 (88)	Costa (2004)

Cuyabano, Ecuador	70 (71)	28 (40)	0 (0)	3 (4)	39 (56)	Poulsen et al. (2006)
Los Volcanes, Bolivia	24 (77)	6 (25)	0 (0)	0 (0)	25 (75)	Linares-Palomino et al. (2008)
Los Volcanes, Bolivia semideciduous	30 (64)	7 (16)	2 (7)	0 (0)	23 (77)	Linares-Palomino et al. (2008)
Los Volcanes, Bolivia evergreen	38 (60)	7 (18)	1 (3)	2 (5)	28 (74)	Linares-Palomino et al. (2008)

Tab. 3. Richness and taxonomic composition of terrestrial understory herb assemblages in tropical forests. Number in parentheses are percentages, for the categories “ferns and lycophytes“ and “angiosperms” these are relative to the total species numbers, for the specific families to the angiosperm number.

Taxonomically, 55% of all terrestrial herb species at both study sites were ferns and lycophytes, and 45% angiosperms. This high proportion of ferns contrasts with previous studies in Southeast Asia, Africa and South America, where the percentage of ferns and lycophytes typically ranges from 10% to 25% (Tab. 3). The only comparably high values have been obtained in a montane cloud forest in the Andes of Venezuela (Kelly et al. 1994), suggesting that the high diversity of ferns may be linked to elevation. Indeed, the diversity of terrestrial ferns typically increases with elevation to around 2000 m, and only declines at higher elevations (Kessler 2001, Kluge et al. 2006). The dominance of Araceae, Orchidaceae, and Zingiberaceae among the angiosperms, all belonging to the monocotyledons, appears to be typical of humid tropical forests, but differs strikingly from dry forests in India (Annaselvam and Parthasarathy 1999, Chittibabu and Parthasarathy 2000, Rasingam and Parthasarathy 2009). Among our two study sites, lower-elevation Pono was more species-rich overall than higher-elevation Bariri, suggesting a pattern of decreasing herb diversity within this elevational range. Proctor et al. (1988) and Poulsen and Pendry (1995), however, found increasing herb diversity on low-elevation mountains in Borneo, suggesting an overall hump-shaped elevational pattern of tropical forest herb diversity with elevation, as has previously been documented for ferns (Kessler 2001, Kluge et al. 2006), epiphytic herbs (Cardelúz et al. 2006), and vascular epiphytes (Krömer et al. 2005) in tropical America.

Biogeographically, Sulawesi is located just east of Wallace's line, the famous biogeographical boundary separating the Malesian zoogeographical region from the Australasian region (Welzen et al. 2005). Although some plant families also follow this break (e.g., Dipterocarpaceae with over 250 species in Borneo and only 6-7 in Sulawesi; Whitten et al. 1987), van Steenis (1950) proposed that the Wallace's Line is not a sharp demarcation for plants

and that it should mainly used to establish faunal provinces. However, Aryanti and Gradstein (2007) recently found that the montane liverwort flora of Mt. Nokilalaki in Lore Lindu National Park was primarily derived from eastern elements and contained few species of western origin, suggesting that the Wallace's Line is also valid for this group of plants. Our study confirmed this pattern for terrestrial ferns, with significantly more species reaching their western than eastern distributional limits on Sulawesi. Because dispersal limitation as such is unlikely to be a limiting factor for spore-dispersed liverworts and ferns, geographical isolation by sea barriers is probably not the main cause for this pattern. Alternative explanations may involve the higher surface area of montane forest habitats in New Guinea as compared to the Greater Sunda islands, differential dispersal determined by prevailing wind streams (e.g., the monsoon), or greater environmental similarity between Sulawesi and New Guinea than to the Greater Sundas (Aryanti and Gradstein 2007).

In conclusion, our study has uncovered an unexpectedly high diversity of terrestrial forest herbs at two sites on the island of Sulawesi. Some of the species in the high number of families found in this study might serve as indicators for global change effects in tropical forests, but this remains to explored with detailed ecological studies.

Biogeographically, there appears to be a more pronounced affinity towards the Moluccas and New Guinea than to the Greater Sundas, although this is based on ferns only and needs to be confirmed for angiosperms. A full understanding of the processes that have generated the high diversity of Sulawesi's plant communities will depend on more comprehensive botanical explorations (Cannon 2001) and the development of phylogenetic hypotheses that will provide data on colonization events as well as the modes and timing of plant diversification.

Acknowledgements

We thank Atok Arianto, Sahar Sabir and Fierdaus for help during field work. Soil data was provided by D. Leitner, M. Bealtzik, O. van Straaten, and E. Veldkamp, and climate data by H. Kreilein, A. Oltchev, and G. Gravenhorst. We are grateful to the STORMA coordination offices in Göttingen, Palu, and Bogor for organisational support, and LIPI for the research permit and supporting field work. This study was funded by the Deutsche Forschungsgemeinschaft (DFG) and the SYNTHESYS Project (http://www.synthesys.info) financed by European Community (NL-TAF-3536).

REFERENCES

Annaselvam J, Parthasarathy N (1999) Inventories of understory plants in a tropical evergreen forest in the Anamalais, Western Ghats, India. Ecotropica 5: 197-211

Aryanti SN, Gradstein SR (2007) Wallace's line and the distribution of the liverworts of Sulawesi. Cryptogamie, Bryologie 28: 3-14

Baas P., Kalkman K. and Geesink R. (eds) 1990. The Plant Diversity of Malesia. Kluwer, Dordrecht, The Netherlands.

Backer CA, Bakhuizen van den Brink RC Jr (1963–1968) Flora of Java, Vol. 1-3. Wolters Noordhoff, Groningen, The Netherlands

Cannon CH (2001) The vegetation of Lore Lindu National Park, Central Sulawesi, Indonesia. The Nature Conservancy, Palu, Indonesia

Cannon HC, Summers MHJR, Kessler PJA (2007) Developing conservation priorities based on forest type, condition, and threats in a poorly known ecoregion: Sulawesi, Indonesia. Biotropica 39: 747-759

Cardelús CL, Colwell RK, Watkins JE Jr (2006) Vascular epiphyte distribution patterns: explain the mid-elevation richness peak J Ecol 94: 144-156

Costa CF, Magnusson W, Luizao RC (2005) Mesoscale distribution patterns of Amazonia understorey herbs in relation to topography, soil and watersheds. J Ecol 93: 863-878

Costa FC (2004) Structure and composition of ground-herb community in a terra-firme Central Amazonia forest. Acta Amazonica 34: 53-59

Chittibabu CV, Parthasarathy N (2000) Understory plant diversity in a tropical evergreen forest in the Kolli Hills, Eastern Ghats, India. Ecotropica 6: 129-140

Flora Malesia, Pteridophyta (Ferns and Ferns Allies) (1981), Vol. 1. National Herbarium Nederland Univeriteit Leiden branch

Flora Malesia, Pteridophyta (Ferns and Ferns Allies) (1991), Vol. 2. National Herbarium Nederland Univeriteit Leiden branch

Flora Malesia, Pteridophyta (Ferns and Ferns Allies) (1998), Vol. 3. National Herbarium Nederland Univeriteit Leiden branch

Gentry AH, Emmons LH (1987) Geographical variation in fertility phenology and composition of the understory of neotropical forest. Biotropica 19: 216-227

Hall R, Holloway JD (Eds.) (1998) Biogeography and geological evolution of SE Asia. Backhuys, Leiden, The Netherlands

Herzog SK, Kessler M, Cahill TM (2002) Estimating species richness of tropical bird communities from rapid assessment data. Auk 119: 749-769.
In den Bosch HAJ (1985) Snakes of Sulawesi: Checklist, Key and additional biogeographical remarks. Zool Verhandel 217: 1-50

Jacobs M. (1988) The Tropical Rainforest. A First encounter. Springer-Verlag, Berlin,Tokyo, 1-295

Kati JS, Cardenas GG, Tuomisto H (2004) Forest classification in an Amazonian rainforest landscape using pteridophytes as indicator species. Ecography 27: 689-700

Kelly DL, Tanner VJ, Nic Lughadha EM, Kapos V (1994) Floristic and biogeography of a rain forest in the Venezuelan Andes. J Biogeogr 21: 421-440

Kessler M (2001) Pteridophyte species richness in Andean forest in Bolivia. Biodiv Conserv 10: 1473-1495

Kessler M, Kessler PJA, Gradstein SR, Bach K, Schmull M, Pitopang R. (2005) Tree diversity in primary forest and different land use systems in Central Sulawesi. Indonesia. Biodiv Conserv 14: 547-560

Kluge J., Kessler M. Dunn R.R (2006) What drives elevational patterns of diversity? A test of geometric constraints climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. Global Ecol Biogeogr 15: 359-371

Krömer T, Kessler M, Gradstein SR, Acebey A (2005) Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. J Biogeogr 32: 1799-1809

Linares- Palomino R, Cardona V, Hennig E I, Hersen I, Hoffmann D, Lendzion J, Soto D, Herzog SK, Kessler M (2008) Non-woody life-form contribution to vascular plant species richness in a tropical America forest. Plant Ecol 201: 87-99

Moss SJ, Wilson MEJ (1998) Biogeography implication of the Tertiary palaeogeographic evolution of the Sulawesi and Borneo. Biogeography and geological evolution of Southeastern Asia. Backhuys, Leiden, The Netherlands

Poulsen AD, Pendry CA (1995) Inventories of ground herbs at three altitudes on Bukit Belalong, Brunei, Borneo. Biodiv Conserv 4: 745-757

Poulsen AD, (1997) Plant diversity in forest of western and eastern Zaire (Preliminary results). AAU reposts 36 Department of Systematic Botany, University of Aarhus.

Poulsen AD, Hafashimana D, Eilu G, Liengola IB, Ewango CEN, Hart TB (2005) Composition and species richness of forest along the Albertine Rift, Africa. Biol Skrifter 55: 129-143

Poulsen AD, Tuomisto H, Balslev H (2006) Edaphic and floristic variation within a 1-ha plot of lowland Amazonian rain forest. Biotropica 38: 468-478

Proctor J, Lee YF, Langley AM, Munro WRC, Nelson (1988) Ecological studies on Gunung Silam. A small ultrabasic mountain in Sabah, Malaysia. Environment, forest structure and floristics. J Ecol 76: 320-40

Rasingam and Parthasarathy (2009) Diversity of understory plants in undisturbed tropical lowland forests of Little Andaman Island, India. Biodivers Conserv 18: 1045-1065

Roos M.C. 1993. State of affairs regarding Flora Malesiana: progress in revision and publication schedule. Flora Malesiana Bulletin 11: 133–142.

Roos CM, Kessler PJA, Gradstein SR, Bass P (2004) Species diversity and endemism of five major Malesian islands: diversity-area relationships. J. Biogeogr. 31:1893-1908

Ruokolainen K, Linna A, Tuomisto H (1997) Use of Melastomataceae and pteridophytes for revealing phytogeographical patterns in Amazonian rain forests. J Trop Ecol 13: 243-256

Schulze CH, Waltert M, Kessler PJA, Pitopang R, Shahabuddin, Veddeler D, Steffan-Dewenter I, Mühlenberg M, Gradstein SR & Tscharntke T (2004) Biodiversity indicator taxa of tropical land-use systems: comparing plants, birds and insects. Ecological Applications 14: 1321-1333.

Sporn SG, Bos MM, Hoffstätter-Müncheberg M, Kessler M, Gradstein SR (2009) Microclimate determines community composition but not richness of epiphytic understory bryophytes of rainforest and cacao agroforest in Indonesia. Funct Plant Biol 36: 171-179

van Steenis CGGJ. (1950) The delimitation of Malaysia and its main plant geographical divisions. Pp. Ixx-Ixxv. In: van Steenis CGGJ (ed.), Flora Malesiana. Series 1, 1. Noordhoff-Kolff, Jakarta, Indonesia.

Walther BA, Moore JL (2005) The concepts of bias, precision and accuracy, and their use in testing the preformance of species richness estimators, with a literature review of estimator performance. Ecography 28: 815-829

Welzen JWC van, Slik F, Alahuhta J (2005) Plant distribution pattern and plate tectonics in Malesia. Biol Skrifter 55: 199-217

White CWM, Bruce M (1986) The Birds of Wallacea. BOU Checklist No. 7. British Ornithologist's Union, London.

Whitmore TC (1987) Biogeographical evolution of the Malay Archipelago. Oxford University Press, Oxford, UK

Whitten AJ, Muslim M, Henderson GS (1987) The Ecology of Sulawesi. Gadjah Mada University Press, Yogyakarta, Indonesia.

Elevational diversity of terrestrial rainforest herbs: When the whole is less than the sum of its parts

Sandra Willinghöfer [1], Daniele Cicuzza[2], Michael Kessler[2]

[1] *Department of Systematic Botany, Albrecht von Haller Institute of Plant Sciences, Untere Karspüle 2, D-37073 Göttingen, Germany,*
[2] *Institute of Systematic Botany, University of Zürich, Zollikerstrasse 107, CH-8008 Zürich, Switzerland.*

In prep for: *Plant Biology*

ABSTRACT

We studied the diversity of herbaceous terrestrial plant species along an elevational gradient in the evergreen forest in Central Sulawesi, Indonesia. We recorded 302 species belonging to 51 families. The most common group were ferns and lycophytes with 62% of the species, followed by monocots with 25% and dicots with 14%. Overall species richness did not show any particular relation with elevation, while the diversity of ferns increased significantly with elevation, monocots did not show a pattern, and dicots showed a hump-shape pattern with maximum richness at 1800 m a.s.l. These patterns in turn were only partly reflected in the patterns of the individual plant families making up each group. The indipendence of different taxa was also reflected in their relationships to environmental factors (temperature, precipitation, area): although each single family is related to one or several factors, at the group level and at the overall level these trends are lost. These results show that interpreting diversity at higher taxonomic level may overlook important information at the family level and raises the biologically intriguing question whether overall patterns of diversity result from a random accumulation of group-speciic patterns or if there is some interaction between groups (e.g., via competion and niche-preemption).

Key Words: Altitude, elevational gradient, terrestrial herbs, tropics, diversity, species richness, Sulawesi, Indonesia.

INTRODUCTION

Tropical rainforests are well known for their enormous plant and animal diversity, which is especially concentrated in mountain regions (Myers *et al.* 2000, Kreft & Jetz 2010). While the number of field studies on tropical plant diversity is constantly increasing, this research effort is taxonomically and ecologically unevenly distributed, focussing among plants especially on trees at the expense of other life forms (lianas, shrubs, terrestrial and epiphytic herbs) (Linares-Palomino *et al.* 2009). Although terrestrial herbs are recognized as an important component in tropical plant communities (Gentry 1995, Gentry & Dodson 1987, Linares-Palomino *et al.* 2009), there are few quantitative studies of the diversity of tropical herbs. The terrestrial layer of herbaceous plant species in tropical forests plays an important role in light limitation and space competition for seedling and juveniles trees (Tsvuura *et al.* 2010), influencing tree regeneration and forest dynamics (Condit *et al.* 2000), but there is very little data on the diversity of terrestrial herb assemblages (e.g., Poulsen & Pendry 1995). Along tropical elevational gradients, for example, there are dozens of studies on the diversity of trees (e.g., Kitayama 1992) and a lesser number on lianas (Homeier *et al.* 2010), ferns (Kluge *et al.* 2006, Kessler *et al.* in press) and epiphytes (Krömer *et al.* 2005 Cardelus *et al.* 2006), but we are aware of only a handful of studies including, though generally not specifically focussing on, terrestrial herbs. Moreover these studies have all recovered different elevational species richness patterns: Poulsen & Pendry (1995) documented a U-shaped pattern along a short elevational gradient (200-850 m) in Borneo, Poulsen *et al.* (2005) a monotonic decline between 770 m and 1520 m in central Africa, Grytnes & Beaman (2006) a hump-shaped pattern along an extensive gradient (0-4094 m) in Borneo, and Desalegn & Beierkuhnlein (2010) a roughly monotonic increase with elevation in Ethiopia (

1200-2700 m). Thus, little is known on how the diversity and community composition of forest herbs change with elevation, whether there is any generality to them, and if these patterns correspond with those of other life forms.

Elevational gradients offer an outstanding opportunity to study and understand patterns of biotic diversity because they represent reproducible environmental gradients that can be replicated across the globe (Lomolino 2001, McCain 2009). Approximately half of all case studies across a wide range of taxa show hump-shaped richness patterns with maximum richness at an intermediate point of the gradient, with the remainder of the studies including monotonic increases or decreases as well as roughly constant numbers (Rahbek, 1995, 2005; McCain, 2007, 2009). The causes for these different patterns are largely unknown but are often taxon-specific and depend on the spatial extent as well as the geographical location of the gradients (Rahbek 2005, Kessler *et al.* in press).

A large number of partly non-exclusive explanations have been proposed for taxon-specific elevational richness patterns, including (i) current climatic variables such as temperature and humidity (Heaney, 2001; Kessler, 2001a; Bhattarai et al., 2004) which in turn determine energy availability and ecosystem productivity (Hawkins *et al.,* 2003; Currie *et al.,* 2004), (ii) spatial aspects including regional area size (Rosenzweig & Ziv, 1999) and geometric constraints (Colwell *et al.,* 2004; Grytnes *et al.,* 2008a), (iii) historical and evolutionary processes (Ricklefs, 2004), and (iv) biotic processes such as the Rapoport rescue hypothesis (Stevens, 1989) or source-sink effects (Grytnes, 2003; Kessler, 2009). All of these factors may covary with both hump-shaped and linear species richness patterns, and discrimination between them is frequently very difficult, especially due to a lack of relevant information. Despite these limitations, there is increasing consensus that there are close links between species richness and climatic factors, and

that factors such as area, geometric constraints and population-level processes at best modify the climate-dependent patterns (Currie & Kerr 2008, McCain 2009, Kessler *et al.* in press).

The aim of the present study was to document the patterns of species richness of terrestrial forest herbs along an elevational gradient on the island of Sulawesi in Indonesia and to identify possible correlations with environmental factors. Specifically, we asked the following questions: (i) How does terrestrial herb diversity change along the elevational gradient? (ii) Do different taxonomic groups show similar patterns? (iii) Which are the environmental and spatial factors correlated with herb diversity?

MATERIAL AND METHODS

Study sites and field sampling

The study was conducted in and around the Lore Lindu National Park (LLNP) in Central Sulawesi (Indonesia). The park encompasses an elevational gradient from 200-2509 m a.s.l., with about 90% of the area above 1000 m. Precipitation ranges from 2000-4000 mm and mean annual temperature from 26-31°C.

Field sampling was conducted at eight different sites covering elevations between 250 m and 2425 m: Saluki, Mount Nokilalaki (subdivided into 4 elevational belts), Pono, Bariri and Mount Rorekatimbu (Tab. 1, Fig. 1). The highest peak in Central Sulawesi is Mount Rorekatimbu (2509 m), so that our transect covered almost the entire elevational range. Sampling was conducted in 2006 at Bariri and from February to April 2008 at the remaining sites. We established a set of three study transects at each locality, with the exception of the summit of Mount Nokilalaki, where only a single transect was placed, resulting in a total of 22

transect (Tab. 1). Each transect consisted of 12 plots of 5 m x 5 m each, separated by intervals of 35 m from each other, resulting in a total transect length of 445 m. Transects were placed in mature forest, avoiding gaps and other anthropogenic and natural disturbances, water-logged soils or open rocks faces.

In each study plot, all terrestrial herb species and the following environmental factors were recorded: elevation, slope. All plant species were collected, subsequently identified where possible to species level, and finally deposited in the following herbaria: Göttingen (GOET), Bogoriense Bogor (BO), Celebense Palu (CEB), Leiden (L), Zurich (Z), and Berkeley (UC; ferns only).

As explanatory variables, we included mean annual temperature, mean annual precipitation, and land surface area. Climatic parameters for each study site were extracted from WorldClim (Hijmans *et al.* 2006). Area was evaluated estimating the island surface of Sulawesi subdivided by elevational belts: 0-500, 501-1000, 1001-1500, 1501-2000, 2001-2500, and 2501-3000 m.

Study site	Coordinates	Elevation (m)	Number of transects	Mean annual precipitation (mm)	Mean annual temperature (°C)
Saluki	1°18’ S, 119°57’E	250-350	3	1890	24.3
Pono	01°29’ S, 120°03’E	850-1120	3	1895	21.3
Nokilalaki	01° 13’ S, 120° 9’ E	1200-1265	3	1820	19.6
Bariri	01°39’ S, 120°10’E	1400	3	1975	19.1
Nokilalaki	01° 13’ S, 120° 9’ E	1400-1490	3	1840	18.9
Nokilalali	01° 14’ S, 120° 9’ E	1800-1880	3	1875	18.3
Nokilalaki	01°14’ S, 120°9’E	2200	1	1940	17.0
Rorekatimbu	1°16’ S, 120°18’E	2350-2425	3	2132	14.1

Table 1. Overview of the study sites, with information on elevation, temperature and precipitation.

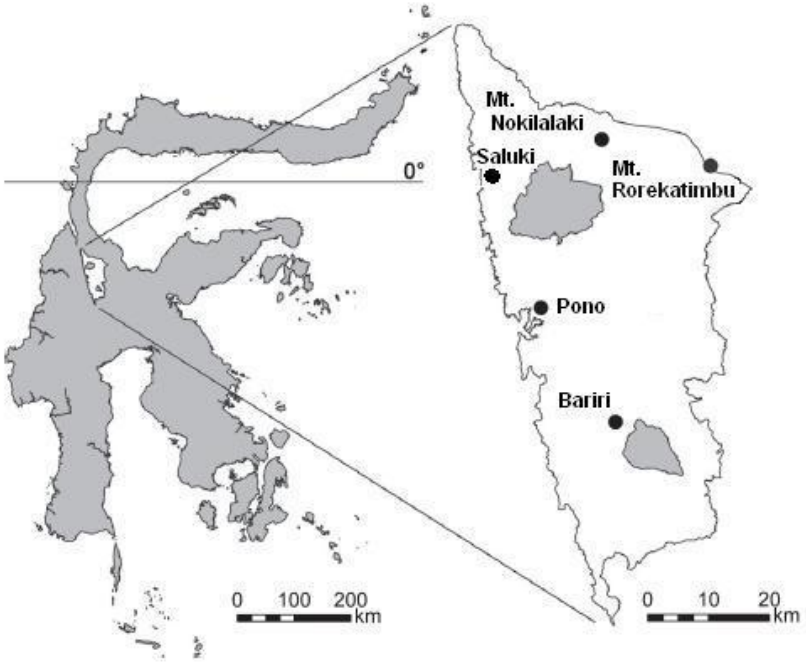


Fig. 1: Location map of the study area (Lore Lindu National Park) and study sites (modified after Culmsee *et al.* 2010).

Statistical Analyses

For the analyses, we calculated the mean number of species per plot for the following taxonomic groups: all terrestrial herbaceous plant species together, separated into three major taxonomic groups (ferns and lycophytes, henceforth called ferns; monocots; dicots), and for the three most species rich families of each of the major groups. Although not monphyletic, we treated ferns and lycophytes as a single group due to the low number of lycophytes and the physiological and ecological similarities between the groups. Likewise, dicots were treated as a group because our sample mainly included eudicots and only x species of basal dicots. To assess the elevational richness patterns of each group, simple linear and polynomial regression models were used to correlate the richness with elevation. Next, stepwise multiple linear regression analyses were used to select the combination of explanatory variables that together best account for herb species richness. Elevation was not included as a variable in these analyses because it does not directly influence species richness (Körner 2000) and because it is closely correlated to temperature. For model selection we use the Akaike Information Criterion (AIC), which incorporates the maximized log-likelihood of the model and a term that penalizes models with greater complexity (Johnson & Omland 2004). Model selection was then based on ΔAIC, which is the difference between the AIC values of the model of interest and the AIC of the best fitting model (Johnson & Omland 2004). All analyses were conducted with R version 2.10 (R Development Core Team 2007), with additional functions provided by the R package vegan (Oksanen *et al.* 2007).

RESULTS

In total, we recorded 302 terrestrial herbaceous plant species belonging to 51 families. Of these, 163 were identified to species level (54%), 97 to genus level (32%) and 42 to family level (14%). Ferns and lycophytes contributed 62% of the species and 41% of the families, monocots 25% of the species and 22% of the families, and dicots 14% of the species and 37% of the families. At the family level, the most species rich fern families were Polypodiaceae (29 species), Aspleniaceae (28) and Dryopteridaceae (16), the most species rich monocot families Araceae (28), Orchidaceae (19), and Zingiberaceae (14), and the most species rich dicots families were Gesneriaceae (8), Begoniaceae (5) and Urticaceae (5).

Among the environmental variables, temperature and elevation ($R = 0.95$, $p < 0.001$) as well the area and elevation ($R = 0.78$, $p < 0.001$) and precipitation with elevation ($R = 0.318$, $p = 0.006$) were strongly correlated. Area were significant correlated to temperature ($R = 0,721$, $p < 0.001$) but not with precipitation ($R = 0.085$, $p = 0.195$), (See Suppl. Mat. Fig. S1).

Mean number of species per plot of all herb taxa combined did not show a significant relationship to elevation ($R = 0.132$, $p = 0.096$) (Fig. 2). However, when we analyzed the three main subgroups separately, we recovered distinct patterns for each of them. Ferns showed a significant increase ($R = 0.603$, $p <0.001$), monocots no clear elevational trend ($R = 0.148$, $p = 0.077$), and dicots a hump-shaped pattern with highest richness at about 1800 m ($R = 0.416$, $p = 0.019$) (Fig. 2). When we further considered the three most species rich families per major taxonomic group, we also recovered distinct patterns. Among ferns, Dryopteridaceae ($R = 0.279$, $p = 0.013$), Aspleniaceae ($R = 0.273$, $p = 0.013$) and Polypodiaceae ($R = 0.202$, $p = 0.036$) all showed elevational increases of species richness (Fig. 2), in accordance to the general patterns of

the ferns. Among monocots, Araceae (R = 0.0714, p < 0.001) and Orchidaceae (R=0.714, p=0.001) showed decreasing richness with elevation, whereas that of Zingiberaceae increased (R = 0.266, p = 0.014) (Fig. 2). Finally, among dicots, Urticaceae showed a significant decrease (R = 0.271, p = 0.013), Gesneriaceae a significant increase (R = 0.545, p < 0.001) and Begoniaceae a non-significant pattern (Fig. 2).

When we used multiple regression models to assess the explanatory power of temperature, precipitation, and area on species richness, for overall herb richness only area was significant (t-value = -2.75, p = 0.013) (Tab. 3, Fig. 3). For ferns we obtained a significant model including area and precipitation (t=-3.56, p=0.002; t=3.144, p=0.006 respectively) while at the family level, richness of Dryopteridaceae was related to temperature (t=1.810, r= 0.08), and Polypodiaceae and Aspleniaceae have both included area (t=-2.348, r= 0.029, t= -3.762, p= 0.001) (Tab.3). The overall monocots pattern was correlated with temperature (t-value = 2.623, p =0.017), while at the family level Araceae were related to temperature (t-value = 2.291, p = 0,034), Orchidaceae to temperature, precipitation and area (t-value = 4.291, p< 0.001; t-value = 3.521, p = 0.002; t-value = -2.37, p = 0.029 respectively) and Zingiberaceae only to area (t-value = -2.452, p = 0.023). The dicots overall showed relations to precipitation and temperature (t-value = -2.420, p < 0.001; t-value = -2.999, t = 0.007), while at the family level Urticaceae were correlated only to precipitation (t-value = -3.133, p = 0.005) and Gesneriaceae and Begoniaceae to precipitation and temperature (t-value = -2.210, p = 0.040, t-value = -5.003, p <0.001; t-value = -3.521, p = 0.002; t-value = -2.554, p = 0.019 respecively) (Tab.3).

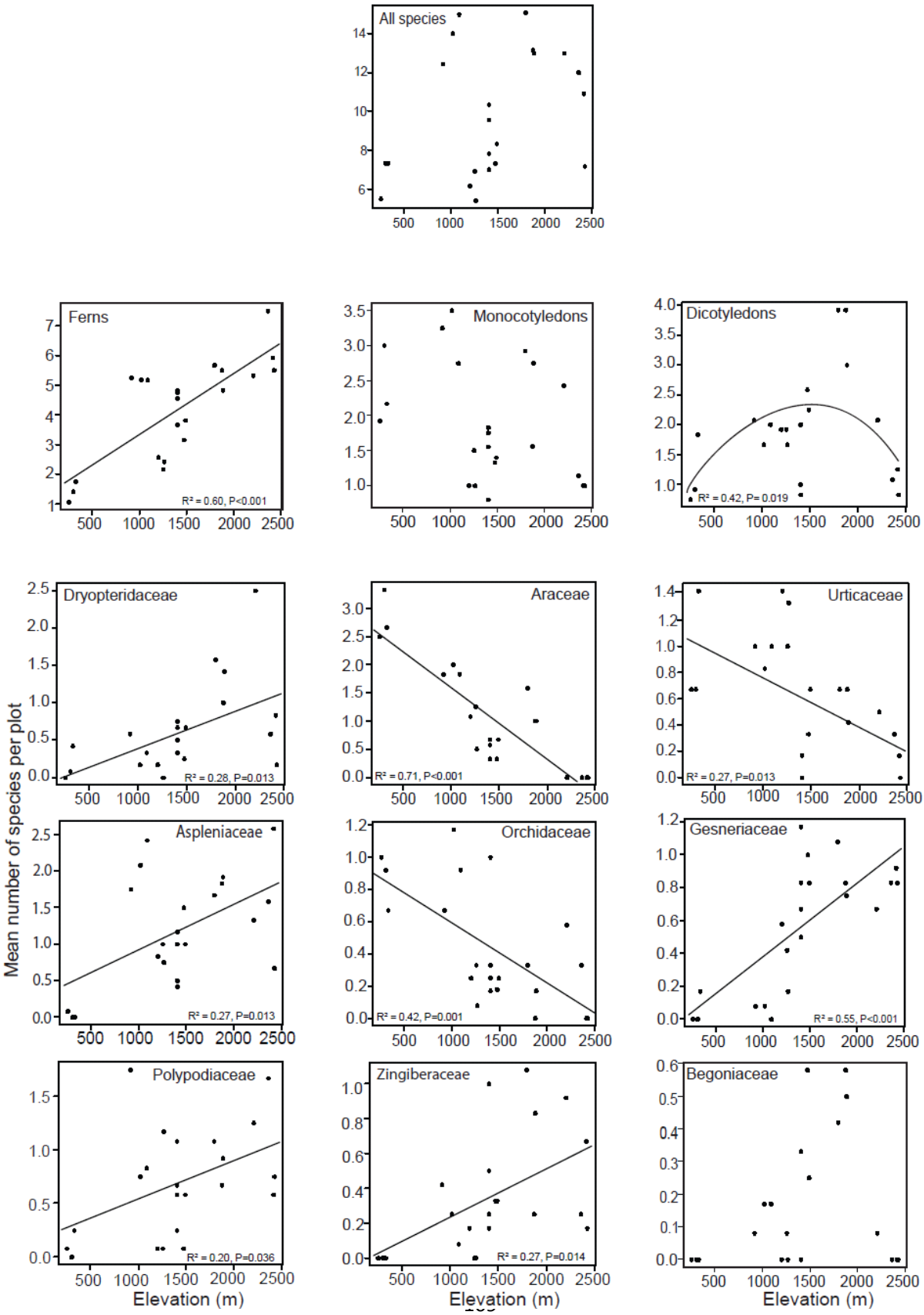

All species
Ferns
R² = 0.60, P<0.001
Monocotyledons
Dicotyledons
R² = 0.42, P= 0.019
Dryopteridaceae
R² = 0.28, P=0.013
Araceae
R² = 0.71, P<0.001
Urticaceae
R² = 0.27, P=0.013
Aspleniaceae
R² = 0.27, P=0.013
Orchidaceae
R² = 0.42, P=0.001
Gesneriaceae
R² = 0.55, P<0.001
Polypodiaceae
R² = 0.20, P=0.036
Zingiberaceae
R² = 0.27, P=0.014
Begoniaceae
Mean number of species per plot
Elevation (m)

Fig. 2. Regression relationships between the mean number of species per plot to elevation for all terrestrial hern species, the three major taxonomic groups and the three most species rich families ine ach of these.

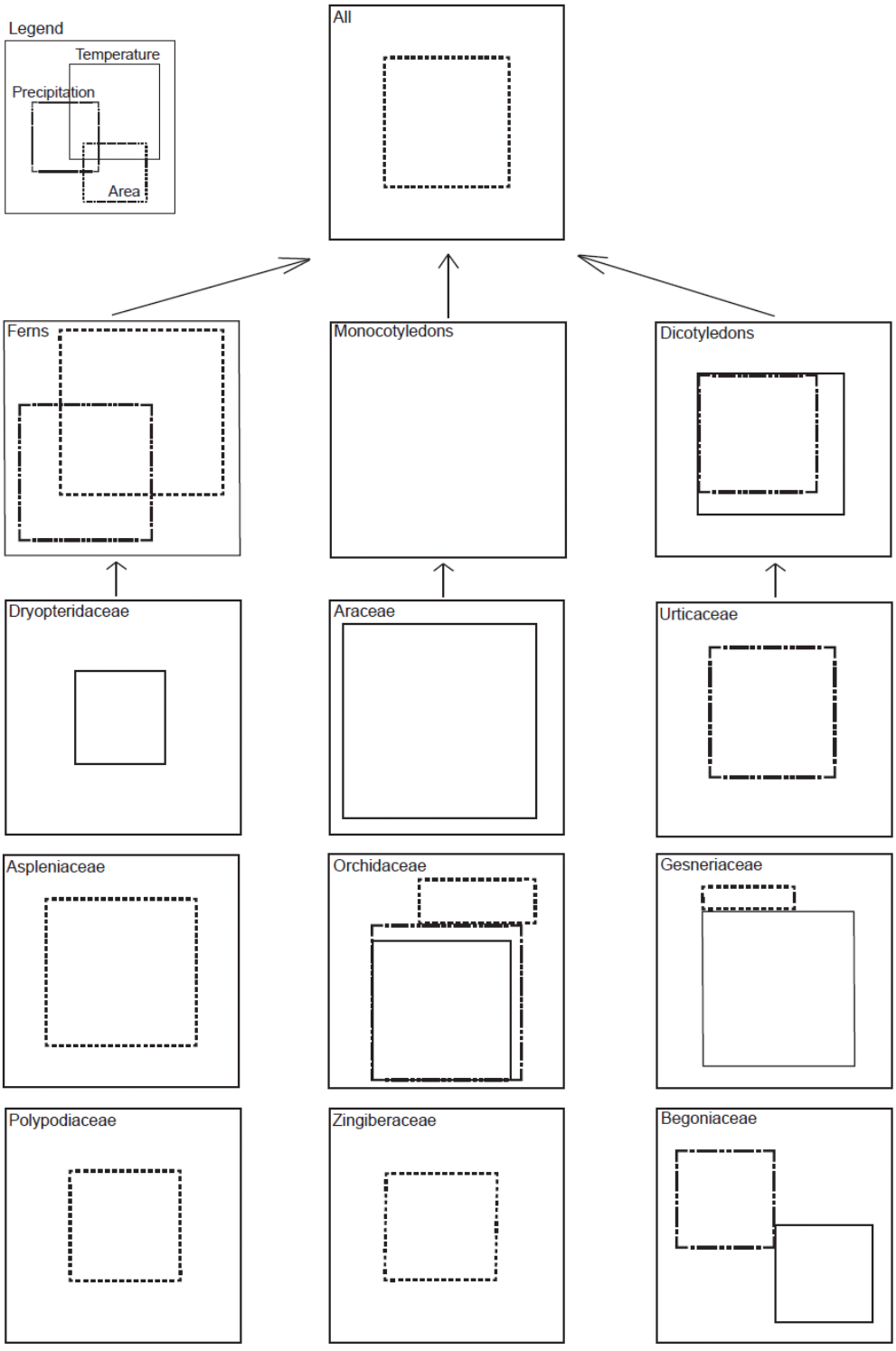

Legend
Temperature
Precipitation
Area
All
Ferns
Monocotyledons
Dicotyledons
Dryopteridaceae
Araceae
Urticaceae
Aspleniaceae
Orchidaceae
Gesneriaceae
Polypodiaceae
Zingiberaceae
Begoniaceae

Fig. 3. Visualization of the explanatory power of the three environmental variables (mean annual temperature, mean annual precipitation, area) on the species richness of all terrestrial herb species, the three major taxonomic groups and the three most species rich families ine ach of these.

Taxa/Family	Factors	Estimate	Standard Error	T value	Pr (>|t|)
Total species	Area	-1.451e-04	5.283e-05	-2.746	0.001
Pteridophytes	Precipitation	1.129e-02	3.589e-03	3.144	0.005
	Area	-6.094e-05	1.723e-05	-3.536	0.002
Dryopteridaceae	Temperature	-0.078	0.043	-1.815	0.084
Aspleniaceae	Area	-1.611e-05	4.282e-06	-3.376	0.001
Polypodiaceae	Area	-7.862e-06	3.348e-06	-2.348	0.029
Monocotiledons	Temperature	4.621e-01	1.762e-01	2.623	0.017
Araceae	Temperature	0.340	0.048	7.110	9.23e-07
Orchidaceae	Precipitation	3.195e-03	9.074e-04	3.520	0.002
	Temperature	2.454e-01	5.718e-02	4.290	0.000
	Area	-1.031e-05	4.356e-06	-2.360	0.029
Zingiberaceae	Area	-5.491e-06	2.240e-06	-2.450	0.023
Dicotyledons	Precipitation	-0.008	0.002	-4.240	0.000
	Temperature	-0.205	0.068	-2.990	0.007
Urticaceae	Precipitation	-0.003	0.001	-3.130	0.005
Gesneriaceae	Precipitation	-0.002	0.001	-2.210	0.039
	Temperature	-0.129	0.026	-5.000	7.9e-05
Begoniaceae	Precipitation	-0.002	0.001	-3.500	0.002
	Temperature	-0.042	0.016	-2.550	0.019

Table 3: Results of the multiple regression models relating the species richness of our study groups to three environmental factors (mean annual temperature, mean annual precipitation, area): Presented are the regression models with the highest AIC values as well as the relative coefficient of determination R^2 and the *p*-value of each regression model.

DISCUSSION

The most striking result of our study is that although total terrestrial herbaceous plant diversity did not show a significant change with elevation, when we analyzed the major taxonomic groups and families independently, most of them showed clear patterns. Or, in other words, the indistinct overall pattern resulted from the accumulation of distinct group-specific patterns. This raises two interrelated questions. First, what are the causes of these group-specific patterns? And second, is the fact that the addition of group-specific patterns results in an indistinct overall pattern a chance event or do the groups interact in some way so that overall herb species richness is restricted to a certain upper bound?

Focussing on the individual groups, in our study terrestrial fern species richness increased with elevation overall as well as among the three most species rich families (Fig. 2). This is a typical pattern in tropical mountains, were species richness of ferns peaks between 1500 m and 2500 m (Kessler *et al.* in press). Monocots showed no clear pattern overall, as a result of family-specific pattern is a decrease for (Araceae, Orchidaceae) and increase for (Zingiberaceae). Araceae are well known to be best represented in humid lowland tropical forests and to decrease in their diversity with decreasing temperatures (Mayo *et al.* 1997), but little is known about

elevational diversity patterns of terrestrial orchids and gingers. These results are supported by the multiple regression model for Araceae with temperature as a significant factor, for Orchidaceae the diversity increase with temperature and area and decrease with precipitation (Tab. S1). The dicots showed a hump-shaped pattern overall, resulting from a combination of decreasing (Urticaceae), increasing (Gesneraiceae) and indistinct (Begoniaceae) patterns. In the regression models the overall dicot richness as well as that of Gesneriaceae and Begoniaceae decreased with the temperature (Tab. S1), precipitation had a negative relationship to the richness of all dicots, Begoniaceae and Urticaceae, while the richness of Gesneriaceae increased with the precipitation. Because of the paucity of studies of tropical forests herbs, we are unable to decide if these patterns are typical for most of the families and if they are representative for tropical environmental. It is noteworthy, however, that several of our models included a negative relationship of species richness to area. While, this result has stitistical significance, it is biologically meaningless since there is no conceivable mechanisms by which increasing area could reduce the species richness of a group. Most likely, this is a spurious result in which area captured part of the variation of species richness that is in effect accounted for by some ecological factor not measured by us (e.g., soil parameters, air humidity).

As detailed in the introduction, the covariance of explanatory factors along elevational gradients ferquently makes it difficult to identify causal relationships. Despite these limitations, there are three non-exclusive major processes that may lead to the observed climate-species richness relationships.

First, the relationship may be determined by the physiological tolerances of the species involved. For example, high temperatures and low air humidity have repeatedly been proposed as limiting fern diversity in lowland tropical forests (Bhattarai *et al.* 2004, Kessler 2001, Kluge *et*

al. 2006) and there is increasing evidence that ferns are less capable of optimising their water-use efficiency than angiosperms (Brodribb & Holbrook, 2004; Brodribb *et al*., 2009). Furthermore, the majority of modern ferns has very sensitive photoreceptors (Doi & Shimazaki 2008). This appears to limit the productivity and competitive ability of many ferns and perhaps concentrates them in more shady and humid environments such as mossy mountain forests. Globally, fern diversity declines more strongly towards arid and cold climatic conditions than that of angiosperm (Kreft *et al*., 2010), further suggesting ferns are physiologically less adaptable. Similar arguments could be made for each of the other taxa, but because the physiologically most suitable climatic conditions are often deduced from where species richness is highest, there is always a risk of circular argumentation.

Second, there may also be an indirect effect of climate via ecosystem productivity (Lieth, 1975; Currie *et al.*, 2004) and hence the energy available for plant growth and development. We are currently unable to assess the importance of productivity on herb richness because of the close covariance of productivity to climate, because we lack productivity measures that are independent of climatic data, and because we do not know what proportion of the overall ecosystem productivity is taken up by the terrestrial herb assemblages and the individual groups at a given site and elevation.

Third, the high species richness of different groups at different elevations may be an evolutionary legacy of longer lineage ages or of higher speciation or lower extinction rates under certain climatic conditions (Jablonski *et al.* 2006, Kozak & Wiens 2010). Testing these hypotheses will require highly resolved and dated phylogenies, which are currently unavailable for our study groups, especially in a taxonomically poorly region as is Sulawesi.

These different processes may have different impacts at different taxonomic levels, which bring us to the question of the causes for the indistinct overall pattern. Ill-defined overall elevational richness patterns of plants resulting from the addition of distinct group-specific patterns have previously been documented by Bhattarai & Vetaas (2003) in Nepal and Desalegn & Beierkuhnlein (2010) in Ethiopia, suggesting that the pattern found by us may be common in tropical mountains. However, Sanchez-Gonzales & Lopez-Mata (2005) found congruent hump-shaped richness patterns for all plants and major groups in Mexico.

We can conceive two fundamentally different ways in which group-specific richness patterns may be added up. First, the individual groups may be independent of each other so that the indistinct overall pattern may simply be result of the random addition of the group-specific patterns. Second, overall herb species richness at a given elevation may be limited by the space or resource availability (Bartels & Chen 2010). In the case that such an upper bound exists, species richness of a given lower-level taxonomic group would not be independent from the diversity of other groups.

These hypotheses could be tested experimentally by, e.g., partly removing the herb vegetation from selected plots and observing the possible invasion by species previously absent. Another option would be to compare biogeographically disparate elevational transects along which the composition of, e.g., monocot families varies, so that the intensity of interfamilial competition would vary. Clearly, species richness patterns of tropical herb species have been largely neglected so far but, as shown in this study, represent a potentially highly interesting field of research that may complement the extensive research conducted especially on trees.

ACKNOWLEDGMENTS

We thank M. Sigit, A. Rahman and W. Lorenz for their coordination in Palu and Göttingen, and the local field assistants for their help during field work. Field work was supported by the STORMA project (Stability of Tropical Rainforest Margins) funded by the German Research Foundation (DFG). Identification of herbaceous species were conducted partly at the Herbarium of Leiden supported by the European project SYNTHESYS (NL-TAF-3536).

REFERENCES

Bartels, S.F. & H.Y.H. Chen. 2010. Is understory plant diversity driven by resource quality or resource heterogeneity? *Ecology* **91**: 1931-1938.

Bhattarai KR, Vetaas OR (2003) Variation in plant species richness of different life forms along a subtropical elevation gradient in the Himalayas, east Nepal. *Global Ecol Biogeogr* **12**: 327-340

Bhattarai, K.R., Vetaas, O.R. & Grytnes, J.A. (2004) Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography* **31**: 389-400.

Brodribb, T.J. & Holbrook, N.M. (2004) Stomatal protection against hydraulic failure: a comparison of coexisting ferns and angiosperms. *New Phytologist* **162**: 663-670.

Brodribb, T.J., McAdam, S.A.M., Jordan, G.J. & Field, T.S. (2009) Evaluation of stomatal responsiveness to CO_2 and optimization of water-use efficiency among land plants. *New Phytologist* **183**: 839-847.

Cardelús, L.C., Colwell, R.K. & Watkins, J.E.Jr. (2006) Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology* **94**: 144-156.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004) The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist* **163**: E000-E023.

Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Itoh, A., LaFrankie, J.V., Lee, H.S., Losos, E., Manokaran, N., Sukumar, R. & Yamakura, T. (2000) Spatial patterns in the distribution of tropical tree species. *Science*, **288**, 1414-1418.

Culmsee, H. Leuschner, C. Moser, G. Pitopang, R. (2010) Forest aboveground biomass along an elevational transect in Sulawesi, Indonesia, and the role of Fagaceae in tropical montane rain forests *Journal of Biogeography*, **37**: 960-974.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T, O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* **7**: 1121-1134.

Currie, D.J. & Kerr, J.T. (2008) Tests of the mid-domain hypothesis: a review of the evidence. *Ecological Monographs* **78**: 3-18.

Desalegn W, Beierkuhnlein C (2010) Plant species and growth form richness along altitudinal gradients in the southwest Ethiopian highlands. *J Veg Sci* **21**: 617-626

Doi, M. & K. himazaki. 2008. The stomata of the fern Adiantum capillus-veneris do not respond to CO_2 in the dark and open by photosynthesis in the guard cells. *Plant Physiology* **147**: 922-930.

Gentry, A.H. & Dodson, C. (1987) Contribution of nontrees to species richness of a tropical rain forest. *Biotropica*, **19**, 149-156

Gentry, A.H. (1995) Patterns of diversity and floristic composition in neotropical montane forests. - In: *Biodiversity and conservation of neotropical montane forests* (ed. by S.P. Churchill, H. Balslev, E. Forero and J.L. Luteyn), pp. 103-126. The New York Botanical Garden, New York.

Grytnes, J.A. (2003) Species richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography* **26**: 291-300.

Grytnes JA, Beaman JH (2006) Elevational species richness patterns for vascular plants on Mount Kinabalu, Borneo. *Journal of Biogeography* **33**: 1838-1849

Grytnes, J.A., Beaman, J.H., Romdal, T.S. & Rahbek, C. (2008a) The mid-domain effect matters: simulation analyses of range-size distribution data on Mount Kinabalu, Borneo. *Journal of Biogeography* **35**: 2138-2147.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guègan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**: 3105-3117.

Heaney, L.R. (2001) Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecology and Biogeography* **10**: 15-39.

Homeier, J., F. Englert, C. Leuschner, P. Weigelt, & Unger, M. (2010) Factors controlling the abundance of lianas along an altitudinal transect of tropical forests in Ecuador. *Forest Ecology and Management* **259**: 1399-1405

Hijmans RJ, Cameron SE, Parra JL et al (2006) The WorldClim interpolated global terrestrial climate surfaces. Version 1.4. http://www.worldclim.org.

Jablonski, D. Roy K. & Valentine J.W. 2006 Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* **314**: 102-106.

Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution*, **19**, 101-108.

Kessler, M., J. Kluge, A. Hemp & R. Ohlemüller. In press. A global comparative analysis of elevational species richness patterns of ferns. *Global Ecology and Biogeography*.

Kessler, M. (2001a) Patterns of diversity and range size of selected plant groups along and elevational transect in the Bolivian Andes. *Biodiversity and Conservation* **10**: 1897-1920.

Kessler, M. (2009) The impact of population processes on patterns of species richness: Lessons from elevational gradients. *Basic and Applied Ecology* **10**: 295-299.

Kiew Rutb, 2005. Begonias of peninsular Malaysia. Natural history publications (Borneo) Kota Kinabalu, Sabah, Malaysia. p 1-308.

Kitayama, K. (1992) An altitudinal transect study of the vegetation of Mount Kinabalu, Borneo. *Vegetatio*, **102**, 149-171.

Kluge J, Kessler M, Dunn RR (2006) What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecol Biogeogr* **15**: 358-371

Körner, C. 2000. Why are there global gradients in species richness? Mountains might hold the answere *Trends in Ecology and Evolution* **15**:513-514.

Kozak, K.H., & Wiens J.J. (2010) Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology letters* **13**: 1378-1389.

Kreft, H. & Jetz, W. (2010) A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, online early.

Krömer, T., M. Kessler, S.R. Gradstein & A. Acebey. 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *Journal of Biogeography* **32**: 1799-1810.

Linares-Palomino, R., Cardona, V., Hennig, E., Hensen, I., Hoffmann, D., Lendzion, J., Soto, D., Herzog, S. & Kessler, M. (2009) Non-woody life-form contribution to vascular plant species richness in a tropical american forest. *Plant Ecology*, **201**, 87-99

Lieth, H. (1975) Modeling the primary productivity of the world. *Primary productivity of the biosphere* (ed. by H. Lieth and R.H. Whittaker), pp. 237-263. Springer, New York.

Lomolino MV (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecol Biogeogr* **10**: 3-13

Mayo S., Bogner, J., Boyce, P.C. (1997) *The genera of Araceae*. Kew Royal Botanical Garden. London, UK.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853-858.

McCain, C.M. (2007) Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography* **16**: 1-13.

McCain, C.M. (2009) Global analysis of bird elevational diversity. *Global Ecology and Biogeography* **18**: 346-360.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., & Stevens, M.H.H. (2007) Vegan: Community Ecology Package. R package version 1.8-8 http://r-forge.r-project.org/project/vegan/.

Poulsen AD, Pendry CA (1995) Inventories of ground herbs at three different altitudes on Bukit Belalong, Brunei, Borneo. *Biodiver Conserv* **4**: 745-757

Poulsen AD, Hafashimana D, Eilu G et al (2005) Composition and species richness of forest plants along the Albertine Rift, Africa. *Biol Skrif* **55**: 129-143

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography* **18**: 200-205.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* **8**: 224-239.

Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters* **7**: 1-15.

Rosenzweig, M.L. & Ziv, Y. (1999) The echo pattern of species diversity: pattern and process. *Ecography* **22**: 614-628.

Sánchez-González A, López-Mata L (2005) Plant species richness and diversity along an altitudinal gradient in the Sierra Nevada, Mexico. Diversity Distrib **11**: 567-575

Sosef, M.S.M. 1996. Begonias and African rain forest refuges: general aspect and recent progress. In: van der Maesen, L.J.G., van der Burgt, X.M. & van Medenbach de Rooy, J.M., Eds., *The Biodiversity of African Plants.* Klumer Academic Publishers, Dordrecht. Pp. 601-611.

Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* **133**: 240-256.

Tsvuura, Z., Griffith, M.E., Gunton, R.M., Franks, P.J. & Lawes, M.J. 2010. Ecological filtering by a dominant herb selevts for shade tolrenace in the tree seedling community of coastal dune forest. *Oecologia* **164**: 861-870.

SUPPORTING INFORMATION

	Temperature	Precipitation	Area
All species			(-) r^2= 0.185
Monocots			
Araceae	(+) r^2= 0.727		
Orchidaceae	(+) r^2= 0.421	(-) r^2= 0.024	(+) r^2= 0.306
Zingiberaceae			(-) r^2= 0.231
Dicots	(-) r^2= 0.002	(-) r^2= 0.245	
Gesneraceae	(-) r^2= 0.481	(+) r^2= 0.044	
Begoniaceae	(-) r^2= 0.003	(-) r^2= 0.120	
Urticaceae		(-) r^2= 0.329	
Ferns		(+) r^2= 0.336	(-) r^2= 0.566
polypodiaceae			(-) r^2= 0.216
Aspleniaceae			(-) r^2= 0.414
Dryopteridaceae	(-) r^2= 0.141		

Tab. S1 Factors resulted from the multiple regression models and their results from the graphical relation.

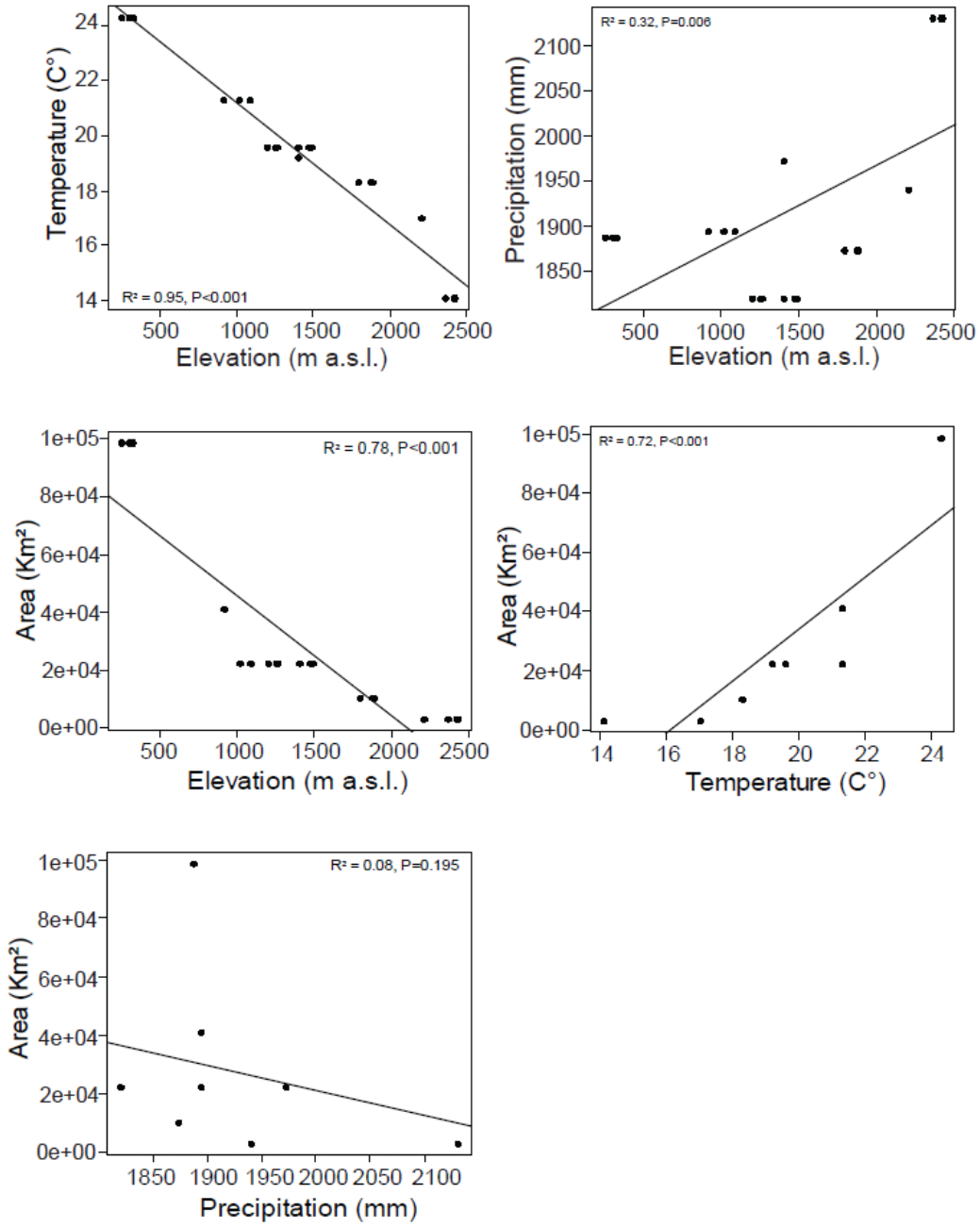


Fig. S1. Pair-wise correlations between the environmental factors considered as explanatory variables for the herb species richness along the elevational gradient in Central Sulawesi.

A transcontinental comparison of the diversity and composition of tropical forest understory herbs

Daniele Cicuzza[1], Thorsten Krömer[2], Axel Dalberg Poulsen[3], Thomas Delhotal[4], Stefan Abrahamczyk[1], Henry Martinez Piedra[5] and Michael Kessler[1]

1 Systematic Botany, University of Zürich, Zürich, Switzerland
2 Centro de Investigaciones Tropicales, Universidad Veracruzana, Interior de la Ex-hacienda Lucas Martín, Privada de Araucarias s/n, Col. 21 de Marzo, C.P. 91019 Xalapa, Veracruz, México
3 Royal Botanic Garden, 20A Inverleith Row, Edinburgh EH35LR, Scotland
4 UFR des Sciences de la Vie et de la Terre, Université Paul Sabatier-Toulouse III 118 route de Narbonne 31062 Toulouse CEDEX 9 France; actual address: Castanet-Tolosan 34 rue du Moulin Courrege 31320 France
5 International Tropical Conservation Foundations (ITCF), 1 Moosmatte 3210 Kerzers Switzerland

Submitted to: *Journal of Biogeography*

ABSTRACT

Aim: To compare the richness and composition of terrestrial herb assemblages in American, African and South East Asian tropical forests.

Location America: Mexico, Costa Rica and Bolivia; Africa: Uganda, Congo and the oceanic island of La Réunion; South East Asia: Peninsula of Malaysia and Indonesia: Borneo (East Kalimantan), Sulawesi and Bali.

Methods: We established 86 non-continuous transects of 445 meters each. Each transect included 12 plots of 5x5 meters each at interval of 35 meters between them. Herbs species diversity was related to six environmental parameters (elevation, actual evapotranspiration (AET), mean annual temperature, minimum temperature of the coldest month, mean annual precipitation, precipitation of the driest month) using minimal adequate regression models (OLS) and simultaneous autoregressive models (SAR). Diversity of family was analyzed among the three continents to highlight the families which are more representative for each continent.

Results: At the global scale, there was a close relationship between herb species richness and elevation as well as AET, with no differences between continents. However, when we subdivided the herb assemblages into three main phylogenetic groups (ferns, monocots, dicots), each groups showed distinct relations to environmental factors and significant differences in richness between continents. Although almost all the families have a pantropical distribution, we found that 12, 11 and 16 families were significantly better represented in America, Africa and Asia, respectively.

Main Conclusions: Overall, tropical forest understory herb diversity increased with increasing elevation and precipitation, as is typical for plants in many situations. Yet, this simply pattern resulted from the addition of group-specific patterns of ferns, monocots and dicots, each of which was represented by a distinct set of families on each continent. This suggests that the diversity of tropical forests herbs may be determined by local ecological factors limiting the number of species that can co-occur at a site. Which species are found at a given site, may in turn reflect group-specific evolutionary and historical factors.

Keywords

Tropical herbs, neotropics, Africa, Asia, climate, autocorrelation.

INTRODUCTION

Tropical rain forests are the most species-rich terrestrial ecosystems (Primack & Corlett 2005). At the same time, there is marked local, regional, and intercontinental variation in the diversity and taxonomic composition of these forests (Corlett & Primack 2006). For example, in Ecuadorian Amazonia about 1000 vascular plant species have been recorded on a single hectare (Balslev *et al*. 1998) while in Bolivia only 670 species are found on the same area (Linares-Palomino *et al.*, 2009). For trees, this spatial variability of species numbers and composition has been widely documented (e.g., Gentry 1988, Pitman *et al.* 2008) and has been linked to differences in climate and soils (Russo *et al.* 2005) as well as to climatic history (Bush *et al.* 2009). Other life forms are much less well studied and global comparisons of species numbers using a consistent sampling method are lacking for terrestrial and epiphytic herbs as well as lianas (Linares-Palomino *et al.*, 2009).

Despite the ecological importance that trees play in tropical ecosystems, the majority of vascular plant species in tropical forests belong to other life forms (Gentry & Dodson, 1987 Balslev *et al.* 1998, Linares-Palomino *et al.* 2009). Depending on forest type and ecological conditions, the relative contribution of terrestrial herbs, shrubs, (Linares-Palomino & Kessler, 2009) lianas, and epiphytes varies considerably (Wolf & Alejandro 2001). Terrestrial herbs typically represent about 45% of the vascular plant diversity in tropical forests (Balslev *et al.* 1998, Linares-Palomino *et al.*, 2009), where they fulfill important ecological roles as food plants for vertebrates and insects (Faveri *et al.* 2008) as well as competitors or facilitators of woody plant seedlings (Metcalfe & Grubb 1995). Despite this importance, to date there has been no

methodologically consistent, intercontinental comparison of the diversity of terrestrial herbs in tropical forests. At the regional scale, the composition of assemblages of terrestrial ferns has been studied in detail in western Amazonia (Tuomisto *et al.*, 2003). Comparable surveys, albeit with lower sample size, have been conducted in central Africa (Poulsen *et al.* 2005) and Borneo (Poulsen & Pendry 1995, Poulsen, 1996). All of these studies found a close link of herb diversity and composition to edaphic conditions, and to a lesser degree to climatic factors.

The aim of the present study was to use a consistent sampling methodology to document patterns of diversity terrestrial herbs in tropical forests in America, Africa and Asia, and to relate these to environmental factors.

MATERIAL AND METHODS

Study areas

Field work was conducted in 1994-1999 in Uganda and Congo and in 2007 and 2008 at the remaining sites. Study sites covered three countries in the Neotropics (Mexico, Costa Rica, Bolivia), three in Africa (Uganda, Congo, the oceanic island of La Réunion), and two in southeast Asia (Malaysia, Indonesia with the islands of Borneo, Sulawesi and Bali) (Fig. 1). The elevation for the localities ranged from 50 m to 2400 m while mean annual precipitation ranged from 733 mm to 4360 mm (Tab. 1). The actual study sites were selected according the following criteria: (1) mature forests, (2) forest structure and canopy cover that were representative of the regional forests, (3) avoiding special microhabitat such as water-logged soils or open rock faces, and (4) minimum distance of 150 m from the forest edge to avoid edge effects.

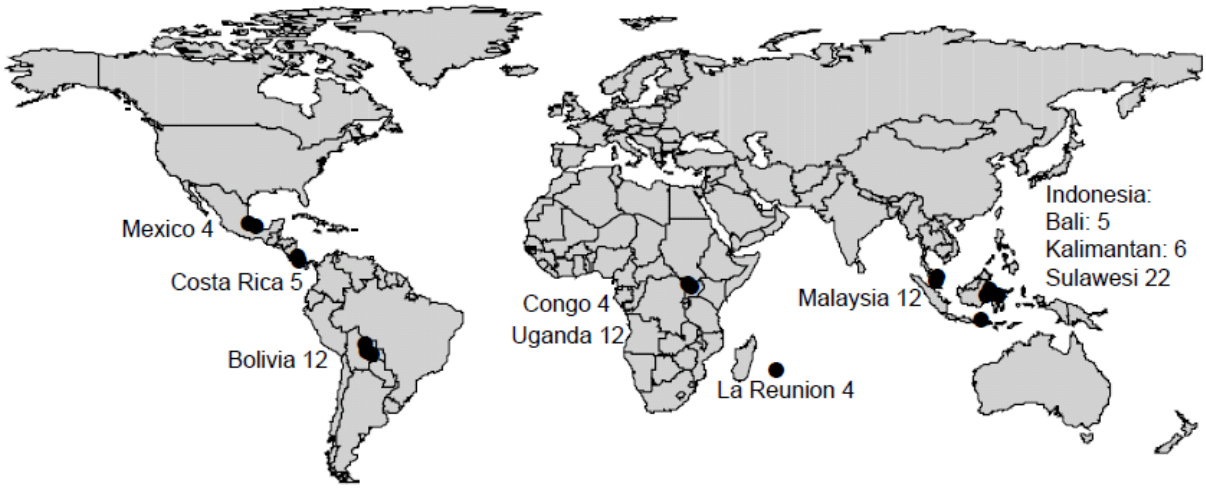


Fig. 1. Location of the study sites indicating the number of transects sampled.

Field sampling and environmental factors

We recorded all terrestrial herbaceous plant species (according to Poulsen, 1996) on 86 transects of 445 meters each. We established 1 to 9 (mean = 3.7) transects per site (Tab. 1). Along each transect we established 12 plots of 5 x 5 m^2 each separated by 35 m from each other. We selected this approach because it allowed us to combine the data from different projects. Further, it allowed us to assess herb diversity at two spatial scales: the 5 x 5 m^2 plots (plot scale) gives an indication of the number of species that directly co-occur and potentially interact while the combination of the 12 plots along a transect (transect scale) provides an approximation of the total number of herb species in a forest site. At two Indonesian sites where we have complete

herb inventories of 1 km^2 of forest (Cicuzza *et al*. 2010), each transect included 19-32% of the total herb richness, while three transects combined included roughly 50%.

All herbs recorded were sorted to morpho-species and determined to family level. While species-level identification was conducted in many cases for the specific projects, a comparison at this taxonomic level is not meaningful for a global analysis such as ours where almost no species are shared between continents. For the analyses, we combined the species for a total number and also separated them into three main groups: ferns and lycophytes (henceforth called ferns for simplicity), monocots, and dicots. Although dicots are not a monophyletic group, in our case this is irrelevant because our sample only included 11 species belonging to the grade of basal angiosperm families.

Species richness was related to six environmental factors: elevation, actual evapotranspiration (AET), mean annual temperature, minimum temperature of the coldest month, mean annual precipitation, and precipitation of the driest month. Elevation was recorded on-site with a hand-held altimeter or GPS. AET was calculated using Turc's formula, where AET = $P/ [0.9 + (P/L) 2]1/2$, with $L= 300 + 25T+ 0.05T3$, $P=$ annual precipitation, and $T=$ mean annual temperature (Turc 1954, González-Espinosa *et al.*, 2004). The climatic factors were extracted from the *WorldClim* model (http://www.worldclim.org/) (Hijmans *et al*. 2004). We did not include all 19 climatic variables provided by *WorldClim* because this would have greatly inflated the number of variables relative to that of sampling sites and because many climatic variables are highly correlated to each other. In addition to annual mean, we included a measure of seasonal aridity (precipitation of the driest month) and of seasonal low temperatures (minimum temperature of the coldest month) because limited water availability and low

temperatures are well known to be related to the diversity of plants and other organisms (Kreft & Jetz, 2007, Hawkins *et al.*, 2003).

Contries	Transects	Elevation (m)	Mean Annual Temperature (°C)	Mean Annual Precipitation (mm)	Coordinates	
Mexico Veracruz (Los Tuxtlas)	2	250	24.5	3507	18° 35' 12.4" N	95° 04' 39.6" W
Mexico Veracruz (Rancho Don Alfonso)	2	1670	16.8	1925	19° 31' 00.3" N	97° 00' 28.2" W
Costa Rica (Reserva de Vida Silvestre Golfito)	4	50	26	4360	8° 38' 19.6" N	83° 10' 00.0" W
Costa Rica (La Selva)	1	50	26	4000		
Bolivia (Río Seco)	4	392	24.1	1085	18° 42' 53.6" S	63° 11' 31.6" W
Bolivia (Santa Cruz)	6	400	24.9	3710	17°46'54.3" S	63° 03' 59.5" W
Bolivia (Buena Vista)	4	425	24.3	733	17° 30' 57.4" S	63° 38' 07.1" W
Uganda (Bwindy)	3	1325	23.1	1375	1° 08' S	29 50' E
Uganda (Kasyoha)	3	1325	23.1	1375	0° 25' S	30° 20' E
Uganda (Kibale)	3	1445	22.2	1500	0° 40' N	30° 35' E
Uganda (Budongo)	3	1445	22.2	1500	1° 55' N	31° 46' E
Congo (Ituri)	4	800	24.2	1672	1° 19' 06.7" N	28° 38' 41.2" E
La Réunion (Mare Longue)	2	250	22.3	4000	21° 10' 56.5" S	55° 21' 48.5" E
La Réunion (Foret de Bebour)	2	1350	16.1	3000	21° 07' 56.5" S	55° 34' 03.3'' E
Malaysia (Taman Negara National Park)	6	200	25.9	2470	4° 23' 19.0" N	102° 24' 0.6" E
Malaysia (Fraser's Hill)	4	1300	20	2660	3° 42' 49.2" N	101° 44' 12.3" E
Indonesia, Bali (Bedugul)	2	600	23.3	1978	8° 16' 45.1" S	115° 10' 59.9" E

Indonesia, Bali (Barat National Park)	3	1500	17.8	2500	8° 08' 14.1" S	114° 28' 28.2" E
Indonesia, Kalimantan (Kutai National Park)	4	300	26.6	1916	0° 31' 42.3" N	117° 28' 48.0" E
Indonesia, Kalimantan (Bukit Bankirai)	2	600	26.2	2304	0° 59' 32.4" S	116° 53' 32.4" E
Indonesia, Sulawesi (LLNP, Saluki)	3	250	27.36	1129	1° 17' 47.1" S	119° 58' 30.6"E
Indonesia, Sulawesi (LLNP, Pono valley)	6	1000	23.44	1800	1° 29' 24.2" S	120° 3' 37.1" E
Indonesia, Sulawesi (LLNP, Bariri)	6	1400	19.56	1850	1° 39' 28.9" S	120° 10' 3" E
Indonesia, Sulawesi (LLNP, Nokilalaki)	3	1800	16.8	1726	1° 14' 36.7" S	120° 9' 5.2" E
Indonesia, Sulawesi (LLNP, Rorekatimbu)	4	2300	15.2	1726	1° 16' 43.2" S	120° 18' 34.3" E

Tab.1. Summary table of the study sites. LLNP = Lore Lindu National Park.

Statistical Analyses

We analyzed species richness at the plot level by averaging the values of each 5 x 5 m^2 of each transect and at the transect level by summing up the species across all 12 plots. In addition we used a measure of beta diversity by dividing the total number of species per transect by the average number of species per plot (*true beta diversity* following Tuomisto 2010).

We used linear correlation analyses between plot diversity and transect diversity, plot diversity and beta diversity, and between transect and beta diversity to assess the relationships between these measures of diversity. Subsequently, we performed simple linear regression analyses between the diversity of herbs at each diversity level and the six environmental variables.

Then, we used stepwise multiple linear regression analyses to select the combination of explanatory variables that together best account for herb species richness. The goodness of fit in relation to the model complexity was evaluated by using the Akaike Information Criterion (AIC), which incorporates the maximized log-likelihood of the model and a term that penalizes models with greater complexity (Johnson & Omland, 2004). Model selection was then based on ΔAIC, which is the difference between the AIC values of the model of interest and the AIC of the best fitting model (Johnson & Omland, 2004). Because spatial autocorrelation violates the assumption of independently distributed errors in regression models, type I errors of traditional tests might be inflated (Legendre 1993). To explore the influence of spatial autocorrelation between the plots we calculated the Moran's I value of the residual of our minimal adequate ordinary least squares regression (OLS) models. Spatial autocorrelation was then included in

simultaneous autoregressive (SAR) models which increase the standard linear regression model with an additional term that incorporates the spatial autocorrelation structure of a given dataset (Arbia *et al.* 2003). The additional term is implemented with a 'spatial weight matrix' where the neighborhood of each location (defined by distance) and the weight of each neighbour need to be defined. The spatial weights matrix in SAR models thus accounts for patterns in the response variable that are not predicted by explanatory variables, but are instead related to values in neighboring locations.

Finally, to assess potential intercontinental differences in herb species richness, we used Analyses of variance (ANOVAs) with post-hoc Tukey honest significance tests to compare the partial residuals from the best fitting models obtained by the stepwise multiple linear regression analysis by grouping the study sites by continent.

Analyses of the family composition of the herb assemblages were conducted using non-metric multidimensional scaling (NMDS), first including all the families and then also separately for ferns, monocots and dicots. Furthermore, to identify the families which play a major role on specific continents, we used the Indicator Species Analysis (Dufrene & Legendre 1997).

All analyses were conducted with R version 2.10 (R Development Core Team 2007), with additional functions provided by the R package vegan (Oksanen *et al.* 2007). The Indicator Species Analysis was performed with PCOrd 5.0 (McCune et al. 1999).

RESULTS

Species richness per transect ranged from a low of 5 along a lowland transect on Borneo to a maximum of 73 species on a transect at 1000 m on Sulawesi. Average numbers of species per plot ranged from 1 to 15.

The correlation analysis between plots and transects diversity showed significant and strongly positive relationships for all the herbs species and for the three major taxonomic groups (Fig. 2). Plot and beta diversity showed a negative relationship for all groups except dicots. Transects and beta diversity were only significantly correlated for monocots (negative) and dicots (positive).

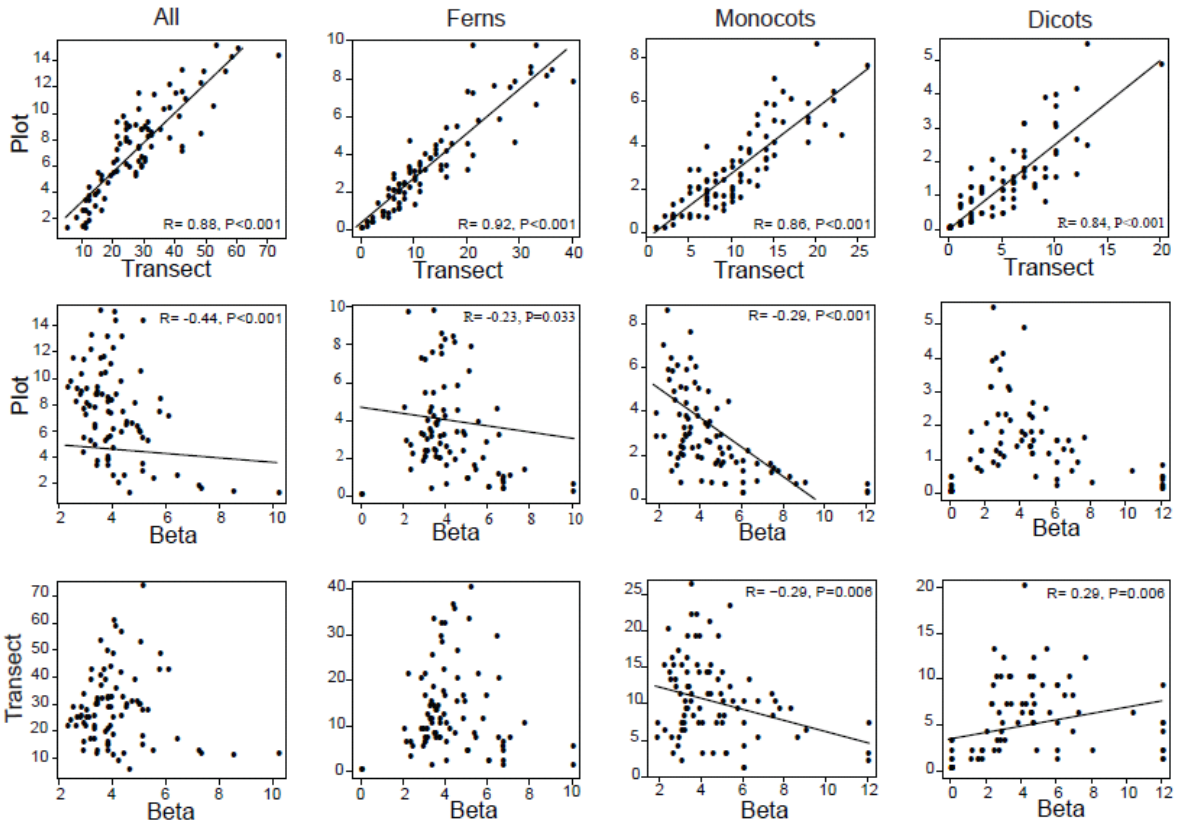


Fig. 2. Relationships between plot, transect and beta diversity of herbaceous species and separately for the three major taxonomic groups. Lines depict significant linear correlations.

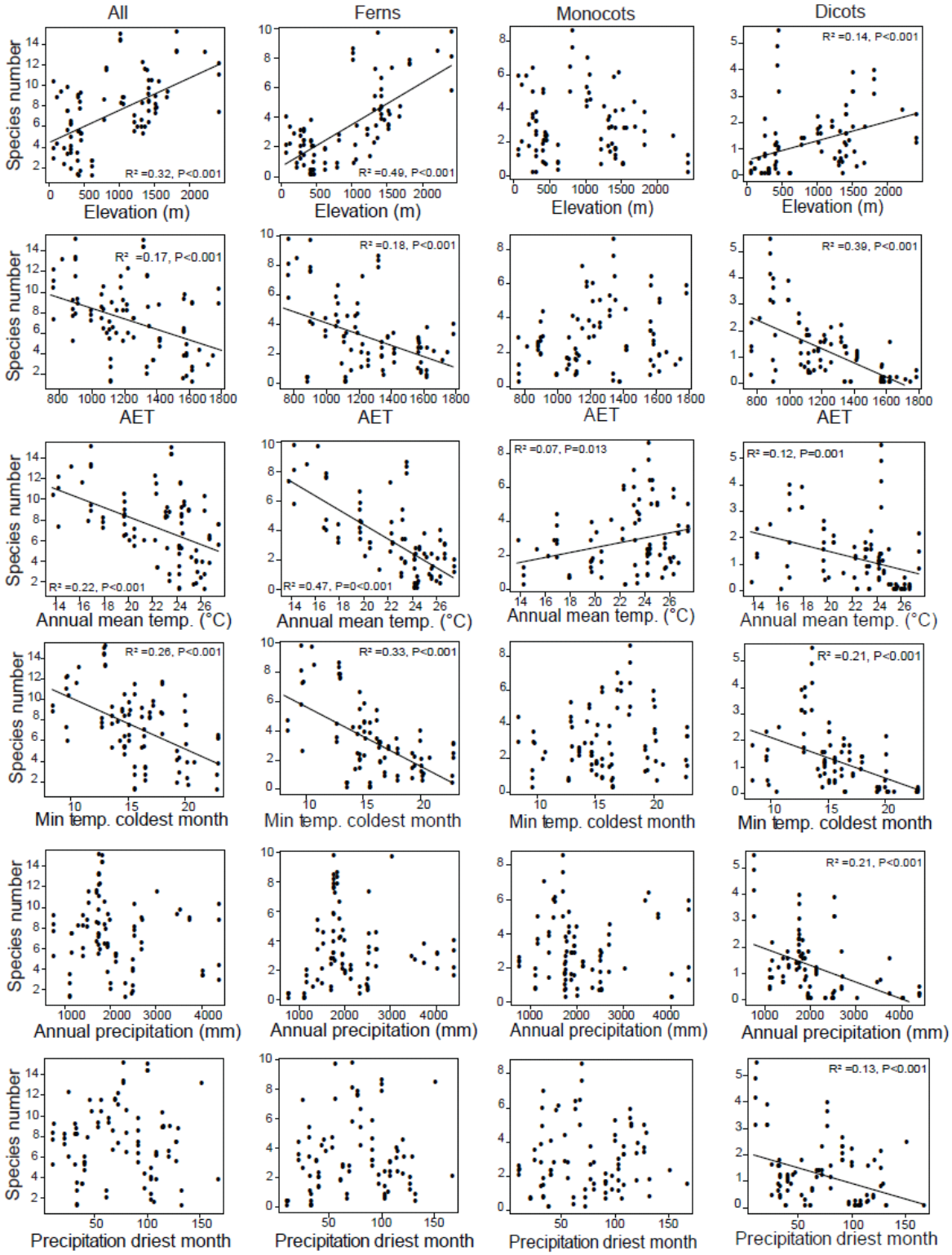

All
Ferns
Monocots
Dicots
Species number
Elevation (m)
R² =0.32, P<0.001
R² =0.49, P<0.001
R² =0.14, P<0.001
AET
R² =0.17, P<0.001
R² =0.18, P<0.001
R² =0.39, P<0.001
Annual mean temp. (°C)
R² =0.22, P<0.001
R² =0.47, P=0<0.001
R² =0.07, P=0.013
R² =0.12, P=0.001
Min temp. coldest month
R² =0.26, P<0.001
R² =0.33, P<0.001
R² =0.21, P<0.001
Annual precipitation (mm)
R² =0.21, P<0.001
Precipitation driest month
R² =0.13, P<0.001

Fig. 3. Linear regression relationships between the mean number of herb species per plot and the six environmental factors included in the analyses.

Considering the pair-wise relationships of herb diversity to the six explanatory variables, at the plot level total herb species richness was positively related to elevation and negatively to AET, mean annual temperature, and temperature of coldest month (Fig. 3). The transect level showed the same results plus a negative relationship with mean annual precipitation (Fig. S1). The species richness of ferns at both the plot and transect levels was significantly positively related to elevation and negatively to AET, mean annual temperature, and temperature of coldest month. The species richness of monocots at the plot and transect levels was only related to mean annual temperature. Finally, for dicots at plot and transect levels we found a significant positive relationship with elevation whereas while for the other five factors the relationship was negative. Beta diversity did not show any significant relationships for all herbs and monocots and weakly significantly ones to mean annual precipitation (postive) for ferns as well as mean annual precipitation and temperature of the coldest month (both negative) for dicots (Fig. S2).

The multiple regression model for the total number of species at the plot and transect levels recovered elevation, precipitation of driest month, mean annual temperature, and minimum temperature of coldest month as significant factors (Tab. 2). Beta diversity was only accounted for by mean annual precipitation and AET (Tab. S1). The model for fern richness at the plot level included elevation and minimum temperature of coldest month, while at the transect level precipitation of driest month was included as third factor. The species richness of monocots was related to elevation and mean annual temperature at the plot levels as well as to

minimum temperature of coldest month at the transect level. Dicots species richness was related to AET, mean annual precipitation and mean annual temperature at the plot level and elevation, AET, mean annual temperature and minimum temperature of the coldest month at the transect level. Beta diversity of ferns and monocots was not significantly related to any factor, while it was weakly related to mean annual precipitation for dicots.

	All species plot		Ferns		Monocots		Dicots	
Variables	OLS	SAR	OLS	SAR	OLS	SAR	OLS	SAR
Elevation (m)	1.02***	0.9**	0.58**	0.59	1.01**	-	0.43.	0.40
AET	-	-0.42	-	-0.41	-	-	-1.43***	-1.59***
Mean annual temperature (°C)	1.14**	1.05**	-	-	1.43**	0.67	1.23**	1.25***
Minimum temperature of coldest month (°C)	-0.53**	-0.54**	-0.44**	-0.63***	-	-	-	-0.02
Mean annual precipitation (mm)	-	0.35***	-	-	-	-	0.41*	0.66**
Precipiation of driest month (mm)	0.23*	0.22	0.29**	-	-	0.41**	-	-0.21
R^2	0.45***	0.46***	0.65***	0.73***	0.21**	0.43***	0.49***	0.55**
AIC	421	422	326	310	348	331	233	228
Moran's I	0.06	0	0.22***	-0.01	0.21***	-0.02	0.13***	0

Tab. 2. Standardized partial regression coefficients of traditional ordinary least squared (OLS) regressions and simultaneous spatial autoregressive error (SAR) models with mean species richness per plot as response variable, and six environmental variables as predictor variables. Minimal adequate OLS models were chosen from the best fitting model based on the Akaike Information Criterion (AIC). The lower spatial autocorrelation of errors in the SAR model confirm that there is no spatial autocorrelation among the plots left in the analyses. *P<0.1, **P<0.001, ***P<0.0001.

The parallel analyses taking into account spatial autocorrelation resulted in roughly similar models (Tab. 2). Overall, spatial autocorrelation was almost fully accounted for in this series of analyses and most SAR models had lower AIC values than their respective OLS counterparts.

The intercontinental comparison of the partial residual from the best fitting models revealed significantly lower fern diversity on the American plots compared to the African and Asian ones, higher diversity of monocots in Africa relative to Asia, and a lower diversity of dicots in Africa compared to America and Asia (Fig. 4). Transect and beta diversity showed similar trends but without significant differences (Figs. S3, S4).

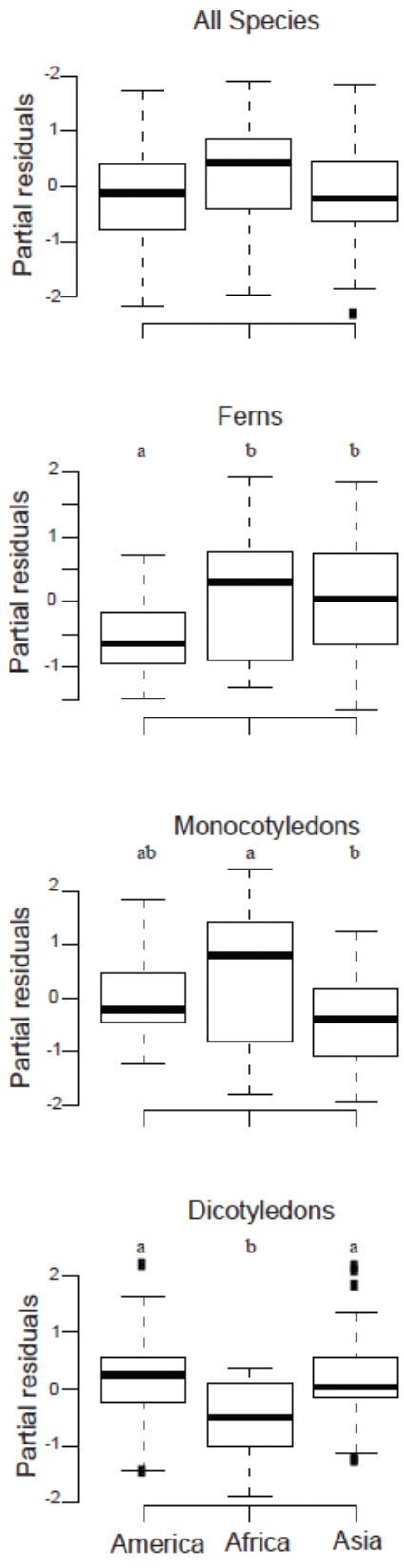

All Species
Partial residuals
-2
1
0
-1
-2
Ferns
a
b
b
Partial residuals
2
1
0
-1
Monocotyledons
ab
a
b
Partial residuals
2
1
0
-1
-2
Dicotyledons
a
b
a
Partial residuals
2
1
0
-1
-2
America
Africa
Asia

Fig. 4. Intercontinental comparison of the partial residuals from the best fitting models. The plots show the herbaceous difference between the three continental tropical forests. Groups with different superscript letters are significantly different from each other (ANOVAs with post-hoc Tukey's HSD). The box plots show the median values (bold line), second and third quartiles (box limits), 95% confidences intervals (whiskers), and outliers (dots).

The non-metric multi dimensional scaling analysis shows that at the family level herb assemblages from the Asian study sites were clearly separated from the African and American ones, while the latter two continents strongly overlapped (Fig. 5). Ferns showed overlaps of all three continents with the American transects slightly separated from those in Africa and Asia. Monocots similarly showed a separation of the American transects but also with only partial overlap of the African and Asian transects. Dicots revealed an even clearer separation of the Asian and Africa transects, with the latter overlapping with the American ones. The Indicator Species Analysis recovered that America had twelve families that were significantly better represented there (1 fern, 7 monocots and 4 dicots), Africa eleven characteristic families (4 ferns, 4 monocots, 3 dicots) and Asia with sixteen such families (7 ferns, 3 monocot and 6 dicots) (Tab. 3).

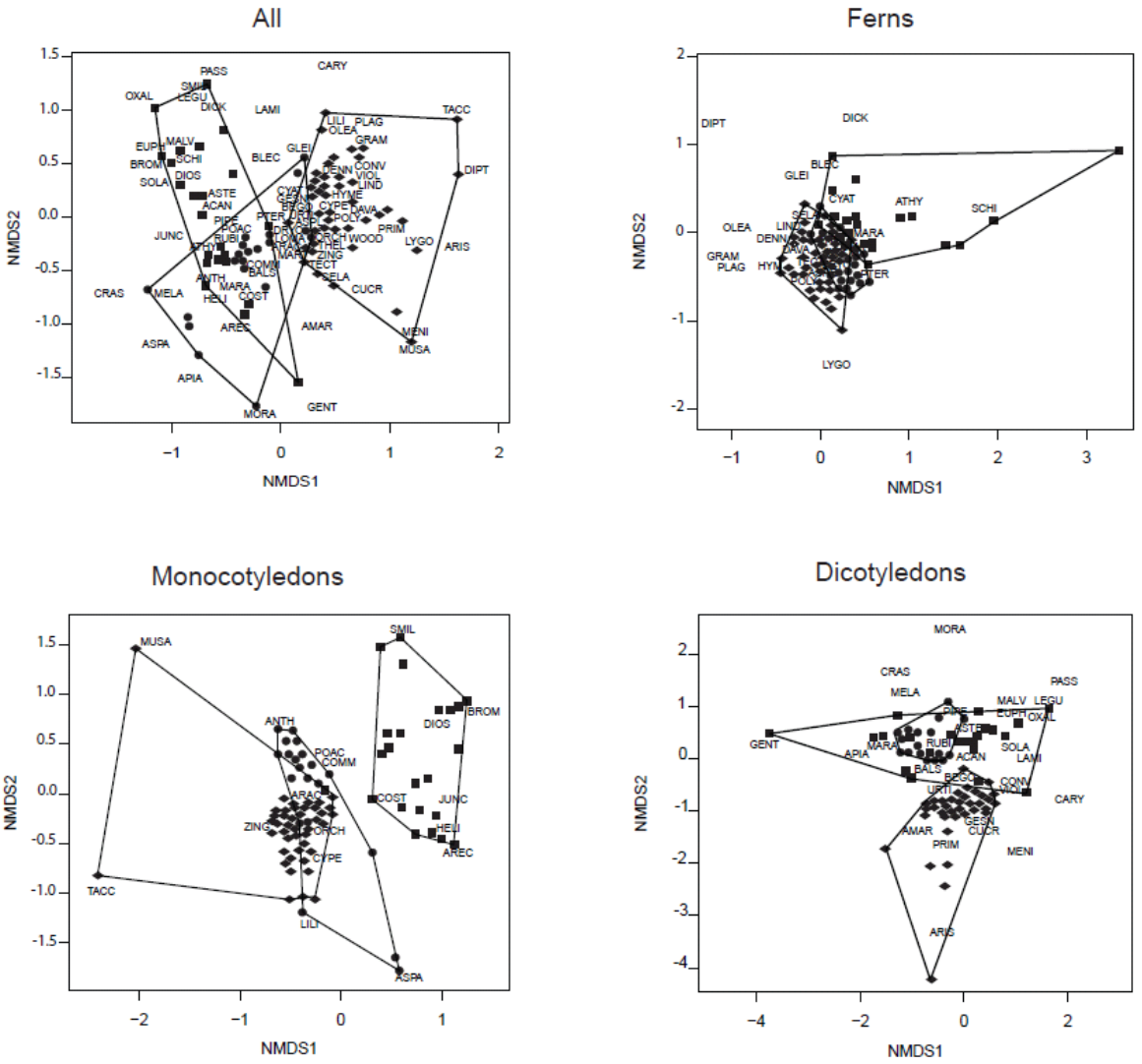


Fig. 5. Non-metric multidimensional scaling of families including all herbs as well as subsets of ferns, monocots and dicots found in our study transects in relation to the transect areas. Squares: America; circles: Africa; rhombs: Asia.

America	Africa	Asia
Acanthaceae***	Agavaceae**	Araceae**
Arecaceae**	Aspleniaceae*	Convolvulaceae***
Bromeliaceae**	Balsaminaceae***	Cucurbitaceae***
Costaceae**	Commelinaceae**	Cyperaceae**
Dioscoridaceae**	Marantaceae**	Davalliaceae*
Euphorbiaceae***	Piperaceae***	Gesneriaceae ***
Heliconiaceae**	Poaceae**	Grammitidaceae*
Juncaceae**	Pteridaceae*	Hymenophyllaceae*
Malvaceae***	Rubiaceae***	Lindseaceae*
Schizaeaceae*	Tectariaceae*	Lygodiaceae*
Smilaceae**	Woodsiaceae*	Plagiogyriaceae*
Solanaceae ***		Primulaceae***
		Selaginellaceae*
		Urticaceae***
		Violaceae***
		Zingiberaceae**

Tab. 3. Results of the Indicator Species Analysis for the 72 families found in the study transects. Families listed are significantly better represented in the transects of the respective continent than in those of the other two continents. *Ferns, ** Monocots, ***Dicots.

DISCUSSION

This is the first transcontinental assessment of the diversity of terrestrial herbaceous plant assemblages in tropical forests. Although there are extensive tropical regions not covered by us, we consider that our 23 study sites provide a representative overview of the diversity of tropical forest herb assemblages. Future studies from additional sites may use our survey as a benchmark against which to assess regional differences in species richness. Patterns of species richness at the plot and transect levels were highly concordant and are hence in the following treated together as "species richness".

We found 5-73 species of terrestrial herbs per transect (300 m^2). This range corresponds to similar variations in species numbers previously detected in local studies, which as few as 26 species recorded on 200 m^2 in Venezuela (Kelly *et al.*, 1994), 27 on 250 m^2 in Borneo (Poulsen & Pendry 1995), 31-63 on 10000 m^2 in Bolivia (Linares-Palomino *et al.*, 2009), 87 on 30000 m^2 in central Amazonia (Costa *et al.* 2005), and 39-42 on 3200 m^2 in southwestern India (Chittibabu & Parthasarathy 2000) to 99 on 10000 m^2 in Amazonian Ecuador (Poulsen & Balslev 1991), 101-117 on 2500 m^2 in Uganda (Poulsen *et al.* 2005), 155 on 1200 m^2 in southwestern India (Annaselvan & Parthasarathy 1999) and 171-203 on 5000 m^2 on Sulawesi (Cicuzza *et al.* 2010). These previous studies used different sampling approaches and are thus difficult to compare directly, but together with our data suggest that the local species richness of terrestrial herbs in tropical forest varies by about an order of magnitude.

Overall, we found that this variation of the local species richness of tropical forest herbs shows a pronounced relationship to elevation, ecosystem productivity and climatic factors.

Although our study did not include soil factors, which are known to strongly relate to the diversity and community composition of tropical herbs (e.g. Tuomisto *et al.*, 2003, Costa 2004, Poulsen *et al.*, 2006)), our models accounted for 21-73% of the variation of species richness between transects, suggesting that the factors assessed by us strongly contribute in determining tropical forest herb diversity. Generally speaking, herb species richness increased with elevation and both precipitation measures and decreased with AET and both temperature measurements. The roughly linear increase of herb species richness with elevation (within the elevational range of our study which reached from 50 m to 2300 m) suggests that along extensive tropical elevational transects, herb species richness will overall show a hump-shaped relationship since it is well known to decline above the treeline (Wesche *et al.* 2008). Such hump-shaped richness patterns are common among plants (Kessler et al. 2001, Grytnes *et al.* 2006) and animals (Graves & Rahbek 2005). The negative relationships of herb species richness to AET and temperature reflect the decline of these variables with elevation in our data set and hence the same general richness-environment relationship. The positive relationship of herb species richness to precipitation corresponds to the well-documented overall increase of plant species richness with water availability both at the local and regional scales (Gentry1988, Kreft & Jetz, 2007).

When we subdivided the herbs into the three main taxonomic groups, ferns and dicots roughly reflected the overall pattern. Ferns, which on average contributed 33% of the herb species in America, 42% in Africa and 50% in Asia, tended to show more pronounced richness-environment relationships than the other group. Ferns are well-known to show hump-shaped elevational richness patterns (Bhattarai *et al.*, 2004, Kluge *et al.* 2006) and to show strong richness-relationships to precipitation and air humidity (Soria *et al.* 2008). At the global scale,

the diversity of ferns declines more pronouncedly towards arid and cold habitats than that of angiosperms (Kreft *et al.* 2010) suggesting that fern species richness is more strongly constrained by extreme climatic conditions. Dicots, which contributed 41% of the species in America, 33% in Africa and 35% in Asia, showed similar patterns as ferns and all herbs combined but had a closer relationship to precipitation values.

Monocots, which contributed 26% of the species in America, 25% in Africa and 17% in Asia, differed markedly from the previous groups in showing poorly defined richness-environment relationships overall and having higher diversity especially in warmer as well as to some degree in higher and seasonally less arid habitats. This reflects the high abundance and diversity of monocot herbs in lowland forests, both in humid ones where they are best represented by members of the Zingiberales (Costaceae, Heliconiaceae, Marantaceae, Zingiberaceae, etc.) (Larsen *et al.* 1998) and the family Araceae (Mayo *at al.* 1997, Mayo *et al.* 1998) as well as in dry ones where grasses (Poaceae) predominate.

The differences between the three major plant groups presumably reflect their physiological tolerances as well as their evolutionary histories. There is increasing evidence that ferns are less capable of optimizing their water-use efficiency than angiosperms (Brodribb & Holbrook, 2004; Brodribb *et al.*, 2009) while at the same time having more sensitive photoreceptors (Schneider *et al.*, 2004). This appears to concentrate ferns in more shady and humid environments than angiosperms. Many monocot families, on the other hand, have originated in the tropics and have had only limited success in adapting to low temperatures, especially frost (Marquez et al. 2006).

Beta diversity was measured by us as the ration between the total number of species on a transect to the mean number of species per plot. Although *a priory* one might expect that this ratio might vary considerably, e.g., if species show more patchy distributions under certain environmental conditions, we essentially found no systematic variation in beta diversity (Tab. S1, Figs. S1, S2). Indeed, species richness at plot scale and transect scales were closely correlated, showing that they reflected the same overall diversity patterns. At different spatial scales, beta diversity may well show regional differences, as shown, e.g., for trees in tropical America by Pitman et al. (Pitman *et al.*, 2008).

Comparing the continents, although overall there were no differences, we found significantly lower fern diversity in America as well as higher monocot and lower dicot species richness than in the other continents (Fig. 5). This suggests that there might be continental deviations in the relative contribution of the three major taxonomic groups. However, in Africa, in particular, our sampling was restricted to few sites and more representative sampling is needed to decide if these trends apply to the continents as a whole or reflect more regional intra-continental patterns. Regardless of the spatial scale of this variation, it is striking that the differences between taxonomic groups counterbalance each other, so that overall we found no difference in herb species richness between continents. This might suggest that the local species richness of tropical herbs is limited by the number of species that can co-occur locally, but that the taxonomic composition may shift, either due to ecological differences between the taxa or as a result of historical factors (Mark, 2002).

Although almost all the families found in our study have pantropical distributions (the main exception being American Bromeliaceae and Heliconiaceae), there is a clear differentiation

of the representation of herb families between the three different continents. Ferns, whose spore dispersal enables them to colonize islands and continents acroos oceans, showed the weakest differentiation between the continents. Nevertheless, the Indicator Species Analysis still recovered eight ferns families as significantly overrepresented on specific continents (4 in Asia, 3 in Africa, 1 in America). American monocots included a distinct group of families (Bromeliaceae and Heliconiaceae). Other monocot families such as Taccaceae, Musaceae, and Zingiberaceae had an Asian center of diversity, but where not recovered as significant in the Indicator Species Analysis because they either also occurring in Africa (Zingiberaceae) or were too rarely recorded in the Asian transects. Among the dicots, America and Africa shared many families while Asian transects were characterized by a set of distinct families.

In conclusion, we found that environmental and geographical factors accounted for a large proportion in the variation of the local species richness of tropical forest herbs and that, when all herbs were analyzed in combination, there were no differences in diversity between the continents. However, when we separated the different taxonomic groups (herbs, monocots, dicots) we found markedly different patterns relative to environmental factors and between continents. Furthermore, continents were characterized by distinct sets of families. These results prompt us to pose the question which factors may determine the local richness of tropical herb assemblages. Assemblages may either be saturated so that the ecologically possible numbers of species as determined by resource availability or heterogeneity actually co-occur. Alternatively, the number of species at different sites may be constrained by evolutionary or historical processes, involving different times since origination or colonization or differences in speciation or extinction rates (Wiens & Donoghue 2004, Jablonski 2008). Our consistent overall pattern

that results from the addition of distinct patterns at the family and clade level suggests that the first of these alternatives may apply. Testing this hypothesis will require experimental studies to determine if tropical herb assemblages are indeed saturated as well as detailed dated phylogenetic trees to assess the evolutionary history of these assemblages.

ACKNOWLEDGEMENTS

We thank R. Linares-Palomino for making available to us the transect data from La Selva and Costa Rica and Sandra Willinghöfer for her help during the field work in Sulawesi. This study was supported by the German Research Foundation (DFG, SFB 552). Identification of herbaceous species were conducted partly at the Herbarium of Leiden supported by the SYNTHESYS project (www.synthesys.info) financed by European Commission (NL-TAF-3536).

REFERENCES

Annaselvan J, & Parthasarathy, N (1999) Inventories of understory plants in a tropical evergreen forest in the Anamalais, Western Ghats, India. *Ecotropica*, **5,** 197-211.

Arbia, G., Griffith, D.A., Haining, R.P. (2003) Spatial error propagation when computing linear combinations of spectral bands: The case of vegetation indices. *Environmental and Ecological Statistics*, **10,** 375-396.

Balslev, H., R.Valencia, C.G. Paz y Mino, H. Christensen, & I.Nielsen. 1998. Species count of vascular plants in one hectare of humid lowland forest in Amazonian Ecuador. *Forest biodiversity in north, central and south America and the Caribbean: Research and monitoring.* (ed. by F. Dallmeier and J. A. Comiskey), pp. 585-594. Man and the Biosphere Series. 21, Unesco and Parthenon, Paris.

Bhattarai, K.R., Vetaas, O.R. & Grytnes, J.A. (2004) Fern species richness along a central himalayan elevational gradient, nepal. *Journal of Biogeography*, **31**, 389-400

Brodribb, T.J. McAdam, S.A.M. Jordan, G.J. Feild, T.S. (2009) Evolution of stomatal responsiveness to CO2 and optimization of water-use efficiency among land plants. *New Phytologist*, **183,** 839-847.

Brodribb, T.J. & Holbrook, N.M. (2004) Stomatal protection against hydraulic failure: a comparison of coexisting ferns and angiosperms. *New Phytologist,* **162,** 663-670.

Bush, M.B., Correa-metrio, A.Y., Hodell, D.A., Brenner, M., Anselmetti, F.S., Ariztegui, D., Mueller, A.D., Curtis, J.H., Grzesik, D.A., Burton, C., & Gilli, A. (2009) Re-evaluation of Climate Change in Lowland Central America During the Last Glacial Maximum Using New Sediment Cores from Lake Peten Itza, Guatemala. *Past Climate Variability in South America and Surrounding Regions: From the Last Glacial Maximum to the Holocene* pp. 113-128 Springer, Berlin, Germnay.

Chittibabu, C.V. & Parthsarathy N. (2000) Understory plant diversity in a tropical evergreen forest in the Kolli hills, Eastern Ghats, india. *Ecotropica,* **6**, 129-140.

Cicuzza, D., Kessler, M. Pitopang, R. Tjitrosoedirdio, S.S. & Gradstein, S.R. (2010) Terrestrial herb of tropical submontane and tropical montane forests in Central Sualwesi, Indonesia. *Tropical rainforest and agroforests under global change* (ed. by T. Tscharntke, C. Leuschner, E. Veldkamp, H. Faust, E. Guhardja, and A. Bidin.) pp. 378-390 Springer, Berlin, Germnay.

Corlett, R.T. & Primack, R.B. (2006) Tropical rainforests and the need for cross-continental comparisons *Trends in Ecology & Evolution,* **21,** 104-110.

Costa, F., Magnusson, R.C., William E. & Luizao, R.C. (2005). Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. *Journal of Ecology*, **93,** 863-878.

Dufrene, M., & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr,* **67,** 345-366.

Faveri, S.B., Vasconcelos, H.L. & Dirzo, R. (2008) Effects of Amazonian forest fragmentation on the interaction between plants, insect herbivores, and their natural enemies. *Journal of Tropical Ecology*, **24,** 57-64.

Gentry, A.H. & Dodson, C. (1987) Contribution of nontrees to species richness of a tropical rain forest. *Biotropica*, **19**, 149-156

Gentry, Alwyn H. (1988) Changes in Plant Community Diversity and Floristic Composition on Environmental and Geographical Gradients. *Annals of the Missouri Botanical Garden* **75,** 1-34.

González-Espinosa, M., María Rey-Benayas, J., Ramírez-Marcial, N., Huston, M.A. & Golicher, D. (2004) Tree diversity in the northern neotropics: Regional patterns in highly diverse chiapas, mexico. *Ecography*, **27**, 741-756

Graves, G.R., & Rahbek, C. (2005) Source pool geometry and the assembly of continental avifaunas. *Proceedings of the National Academy of Sciences of the United States of America*, **102,** 7871-7876.

Grytnes, J.A. & Beaman, J.H. (2006) Elevational species richness patterns for vascular plants on Mount Kinabalu, Borneo. *Journal of Biogeography*, **33,** 1838-1849.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., GuéGan, J.-F.O., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105-3117.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2004) *The WorldClim interpolated global terrestrial climat surfaces*, version 1.3. Available at: http://biogeo.berkeley.edu/.

Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution*, **19**, 101-108

Kluge., J., Kessler, M., & Dunn, R.R. (2006) What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in costa rica. *Global Ecology and Biogeography*, **15**, 358-371

Kelly, D.L., Tanner, E.V.J., Lughadha, E.M.N. & Kapos, V. (1994) Floristics and biogeography of a rain forest in the venezuelan andes. *Journal of Biogeography,* **21**, 421-440

Kessler, Michael Parris, Barbara S. Kessler, Elke (2001). A Comparison of the Tropical Montane Pteridophyte Floras of Mount Kinabalu, Borneo, and Parque Nacional Carrasco, Bolivia. *Journal of Biogeography*, **28**, 611-622.

Kreft, H. & Jetz, W. (2007) Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 5925-5930

Kreft, Holger, Jetz, Walter, Mutke, Jens, Barthlott, Wilhelm (2010) Contrasting environmental and regional effects on global pteridophyte and seed plant diversity. *Ecography,* **33**, 408-419.

Larsen, K., Lock, J.M. Maas, H., & Maas, P.J.M. (1998) Zingiberales. *The Families and Genera of vascular plants* pp. 474-495 Springer, Berlin, Germany.

Legendre P. (1993) Spatial autocorrelation- trouble or new paradigm. *Ecology*, **74**, 1659-1673.

Linares-Palomino, R., Cardona, V., Hennig, E., Hensen, I., Hoffmann, D., Lendzion, J., Soto, D., Herzog, S. & Kessler, M. (2009) Non-woody life-form contribution to vascular plant species richness in a tropical american forest. *Plant Ecology*, **201**, 87-99

Linares-Palomino, R. & Kessler, M. (2009) The role of dispersal ability, climate and spatial separation in shaping biogeographical patterns of phylogenetically distant plant groups in seasonally dry andean forests of bolivia. *Journal of Biogeography*, **36**, 280-290

Mayo S., Bogner, J., Boyce, P.C. (1997) *The genera of Araceae*. Kew Royal Botanical Garden. London, UK.

Mayo S., J. Bogner and PC. Boyce, (1998) Araceae. *The Families and Genera of vascular plants* pp. 26-73 Springer, Berlin, Germany.

Mark, B.B. (2002) Distributional change and conservation on the andean flank: A palaeoecological perspective. *Global Ecology & Biogeography*, **11**, 463-473

Marquez, E.J., Rada, F. & Farinas, M.R. (2006) Freezing tolerance in grasses along an altitudinal gradient in the Venezuelan Andes. *Oecologia,* **3**, 393-397

Mc Cune, B. & Mefford. M.J., (1999) PC-ORD Multivariate analysis of ecological data. Version 5. MjM Software Design, Gleneden Beach OR

Metcalfe, D.J. & Grubb, P. J. (1995) Seed mass and light requirements for regeneration in southeast-Asian rain-forest Canadian *Journal of Botany-Revue Canadienne De Botanique,* **73**, 817-826.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., & Stevens, M.H.H. (2007) Vegan: Community Ecology Package. R package version 1.8-8 http://r-forge.r-project.org/project/vegan/.

Pitman, N.C.A., Mogollón, H., Dávila, N., Ríos, M., García-Villacorta, R., Guevara, J., Baker, T.R., Monteagudo, A., Phillips, O.L., Vásquez-Martínez, R., Ahuite, M., Aulestia, M., Cardenas, D., Cerón, C.E., Loizeau, P.A., Neill, D.A., Núñez V, P., Palacios, W.A., Spichiger, R. & Valderrama, E. (2008) Tree community change across 700 km of lowland amazonian forest from the andean foothills to brazil. *Biotropica*, **40**, 525-535

Poulsen, A.D. & Balslev, H. (1991) Abundance and cover of ground herbs in an Amazonian rain forest. *Journal of Vegetation Science,* **2**, 315-322.

Poulsen, A.D. & Pendry, C. A. (1995) Inventories of ground herbs at three altitudes on Bukit Belalong, Brunei, Borneo. *Biodiversity and Conservation*, **4**, 745–757.

Poulsen, A.D. (1996) Species richness and density of ground herbs within a plot of lowland rainforest in north-west borneo. *Journal of Tropical Ecology*, **12**, 177-190

Poulsen, A.D., Hafashimana, D., Eilu, G., Liengola, I.B., Ewango, C.E.N. & Hart, T.B. (2005) Composition and species richness of forest plants along the Albertine Rift, Africa. *Biologiske Skrifter*, **55**, 129–143.

Poulsen, A.D., Tuomisto, H. & Balslev, H. (2006) Edaphic and floristic variation within a 1-ha plot of lowland amazonian rain forest1. *Biotropica*, **38**, 468-478

Primack, R., & Corlett, R. (2005) Tropical rain forest. Blackwell publishing

Turc, L. (1954) Le bilan d'eau des sols: relation entre les précipitation, l'evaporation et l'acoulement. *Annales Agronomiques*, **5**, 491-596.

R DEVELOPMENT CORE TEAM. 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org

Russo, S.E., Davies, S.J., King, D.A., & Tan, S., (2005) Soil-related performance variation and distributions of tree species in a Bornean rain forest *Journal of Ecology*, **93,** 879-889.

Schneider, H., Russell, S.J., Cox, C.J., Bakker, F., Henderson, S., Rumsey, F., Barrett, J., Gibby, M. & Vogel, J.C. (2004) Chloroplast phylogeny of asplenioid ferns based on rbcl and rnl-f spacer sequences (polypodiidae, aspleniaceae) and its implications for biogeography. *Systematic Botany*, **29**, 260-274

Soria-Auza, Rodrigo W., Kessler, Michael (2008) The influence of sampling intensity on the perception of the spatial distribution of tropical diversity and endemism: a case study of ferns from Bolivia. *Diversity and Distributions*, **14**, 123-130.

Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003) Dispersal, environment, and floristic variation of western amazonian forests. *Science*, **299**, 241-244

Turc, L. (1954) Le bilan d'eau des sols: relation entre les précipitation, l'evaporation et l'ecoulement. *Annales Agronomiques*, **5**, 491–596.

Wesche K., Cierjacks A., Assefa Y., Wagner S., Fetene M. & Hensen I. (2008) Recruitment of trees at tropical alpine treelines: Erica in Africa versus Polylepis in South America. *Plant Ecology & Diversity*, **1,** 35-46.

Wolf, J. H. D., Alejandro, F. (2003) Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography* **30**: 1689-1707.

SUMMARY

This thesis is an ecological study on terrestrial herbaceous species richness in tropical forests of Central Sulawesi (Indonesia) and their adjacent cacao agroforestry systems.

The first two chapters investigate the herb composition in the cacao agroforetry system surrounding the Lore Lindu National Park (LLNP). In addition, I analyze how species composition and abundance changes over time (years) according to different agricultural management practices. The third and fourth chapters investigate the native forest herbs present in two localities and along an altitudinal gradient from the lowland to the highest peak in the central Sulawesi mountain chain. Chapter five compares the tropical herb diversity between the three tropical continents (America, Africa and Asia).

Herbaceous diversity in agroforestry system

In **chapter one,** I studied the terrestrial herb composition in the cacao agroforestry system in two valleys in Central Sulawesi. The plantations selected have different structural conditions and different histories. Overall in the 86 plots I found 91 terrestrial herbaceous species, the number is lower than other published studies conducted both in India and Brazil. Comparing the species number with forest ecology found inside the plantation, with the herbs found in the closed tropical forest inside the national park, I observed that the plantation harboured only 21 species with forest ecology. Species found in adjacent tropical forest equaled to 171 and 203 species in two sites close to the cacao study area. Highest herb diversity among the cacao plantations was found in plantations which harbored a high number of native forest trees. Herb diversity was correlated with light intensity at ground level, where higher light intensity influences the presence of species with a wider distribution and ecological characteristics. Overall highest native herb diversity was found in the plantation containing the highest number of native forest trees, at higher elevation, and with a steep slope, the latter two factors related to aspect and not to the recent conversion to agroforestry. Comparison of herb diversity with the different structural categories (rustic, shade or technified) revealed that greater native herb diversity was found in

the rustic cacao plantations, while higher numbers of weedy pantropical species were found in the technified cacao. We therefore conclude that an intense cacao agroforestry system (i.e. technified) has a very limited value for conservation of herbaceous native species in central Sulawesi.

In **Chapter two** I show the results obtained treating the cacao agroforestry system with two different management's regimes. Plantations were treated with high/low fertilization frequency and high/ low weeding frequency. I found, in the permanent plots, over the two year of experiment an overall diversity of 111 herbaceous species. Species composition was altered by the weeding frequency, particularly after two years of low weeding management I observed new growth of non-annual herbaceous species. The two regimes with high and low frequency of treatment did not alter the overall species composition between light- versus shade-loving species or widespread versus Malesian species over the course of the experiment. Moreover, the fertilization did not increase the species composition significantly, while above and below ground biomass was positively influenced.

In conclusion, I found that the herb assemblages in the studied cacao agroforests were strongly influenced by mechanical weeding and slightly by fertilization. Therefore the frequency of weeding has an impact on the species composition and also on the change in abundance of herbs cover; this result could have an important consequence on the dynamics of population for insect and small vertebrate, altering the whole cacao agroforestry system.

Herbaceous diversity in tropical forest

The herbaceous species composition in tropical rain forest in the Lore Lindu Nation Park showed a high diversity in species composition. In **chapter three** I studied the species diversity and composition of two tropical forest sites; Pono and Bariri, 1000 and 1400m s.sl. respectively. At the Pono site I recognized 91 angiosperm herbs species belonging to 28 families, and 112 fern and lycophyte species from 15 families, resulting in a total of 203 terrestrial herb species overall. While in Bariri I recognized a total of 171 terrestrial herb species, corresponding to 77 angiosperms from 25 angiosperm families and 94 fern and lycophyte species from 20 families. At both sites most fern and lycophyte species had distribution ranges covering the entire

Malesian Region and often extending to Indochina. However, at Pono no fewer than 7 species (13%) are currently considered to be endemic to the island of Sulawesi, whereas no such species were recorded at Bariri. The number of geographically widespread species (tropical Asia to pantropical) was limited at both sites. Biogeographically, there appears to be a more pronounced affinity towards the Moluccas and New Guinea than to the Greater Sundas, although this is based on ferns only and needs to be confirmed for angiosperms

The forest diversity along the altitudinal gradient in central Sulawesi also showed high herb species richness. In **chapter four** the study of terrestrial herbs was conducted along an altitudinal gradient from 250 to 2450 m a.s.l.. Species were classified at the family level, at the group level (ferns, monocotyledons and dicotyledons) and the overall diversity. In total 302 terrestrial herbaceous plant species belonging to 51 families were identified. Overall species diversity did not correlate with elevation and the three plant groups displayed different distribution patterns. Specifically, ferns showed a simple linear regression, no correlation was found for monocotyledons and dicotyledons showed a hump-shaped curve showed maximum diversity at 1700 m a.s.l. Furthermore, analysis of the different distributions for the three most common families present in each plant category also showed family-specific distributions. All the three common ferns families have a positive trend with elevation. The diversity for the monocotyledon families as: Araceae and Orchidaceae decreases with elevation while increase for Zingiberaceae. The dicotyledons diversity at the family level shows for Gesneriaceae an increase with elevation, the Urticaceae a decrease and Begoniaceae not correlated to elevation changes. A possible reason why overall species diversity was not correlated with elevation may be due to the interaction of factors such as temperature and precipitation. The interaction is not apparent clear when diversity is analyzed at higher level as ferns, monocots or dicots. Additionally, physiological tolerance may determine the species composition. For example high humidity is vital for ferns diversity while high temperatures and high humidity are important for Araceae. We can hypothesize that high species richness at different elevations can be explained as a high rate of speciation under certain climatic conditions. These hypotheses however have still to be tested and until the flora of Sulawesi is better known, they remain simply as hypotheses.

Diversity of tropical terrestrial herbs among the three continents using the same methodological sampling design has been a difficult task for many years. In **chapter five** I studied the tropical herbaceous diversity in America, Africa and Asia and compared this diversity with six environmental factors: elevation, actual evapotranspiration (AET), mean annual temperature, minimum temperature of the coldest month, mean annual precipitation, and precipitation in the driest month. Species richness at the plot level showed that diversity was positively related to elevation and negatively related to AET, mean annual temperature, and the temperature of coldest month. These results show that high diversity was found at mid-high elevation and not too lower temperature during the coldest month. The intercontinental comparison showed fern diversity to be lower on the American plots compared to the African and Asian ones. Monocotyledon diversity was higher in Africa relative to Asia, while dicotyledons a lower diversity in Africa compared to America and Asia. The species richness of tropical herbs was largely explained by environmental and geographical factors. When this diversity is observed a higher taxonomic levels (ferns, monocots, dicots) different patterns were observed relative to environmental factors and between continents. Specifically continents were dominated by a particular set of families. These results advices us to further questions, which factor determines the local richness of tropical herb assemblages. The assemblage can be complete and the possible number of species is determined either by the resource availability or due to historical processes, as colonization process, differences in speciation and extinction rates. These hypotheses can be tested with more experimental studies determine if tropical herb assemblages are indeed saturated as well as detailed dated phylogenetic trees to assess the evolutionary history of these assemblages.

ZUSAMMENFASSUNG

Tropische Wälder sind bei weitem die artenreichsten, terrestrischen Ökosysteme unseres Planeten. Unser Wissen über terrestrische Kräuter in tropischen Wäldern als auch in Agroforstsystemen ist immer noch sehr begrenzt. Agroforstsysteme, repräsentiert durch Kakao- und Kaffeeplantagen benötigen Beschattung durch höhere Bäume, um sich zu entwickeln. Aufgrund ihrer Struktur bilden Agroforstsysteme ein waldähnliches Habitat und können potentiell als Lebensraum für viele tropische Arten dienen. Daher ist es wichtig die Bedeutung von Agroforstsystemen zu kennen, um ihren Einfluss für den Artenschutz bewerten zu können.

In dieser Doktorarbeit beschäftigen wir uns mit der Zusammensetzung und Verbreitung terrestrischer Kräuter, sowie mit den Umwelteinflüssen, denen sie ausgeliefert sind. Wir untersuchten die Diversität von Kräutern in tropischen Wäldern und in Kakaoplantagen in Zentralsulawesi, Indonesien, die einen wichtigen Teil Kulturlandschaft in Sulawesi darstellen.

Die Kräuterdiversität in Agroforstsystemen wurde in zwei verschiedenen Tälern untersucht und mit zwei benachbarten Wäldern verglichen. Dabei wurden 91 terrestrische Krautarten festgestellt. Nur 21 der gefundenen Arten kamen auch in den nahe gelegenen Wäldern vor. Die meisten Waldkräuter kamen in Plantagen mit einer hohen Anzahl von Waldbäumen vor. Außerdem nahm die Zahl der Waldkräuter mit zunehmender Höhe und Hangsteigung zu. Die Anzahl der Waldarten in den Plantagen hing nicht vom Alter das Plantage oder der vorherigen Landnutzung ab.

Wir haben verschiedene Plantagen mit unterschiedlichem Management (unterschiedliche Intensität von Düngen bzw. Mähen) untersucht, um dessen Einfluss auf die Artenzusammensetzung und Abundanz abzuschätzen. Selteneres Mähen erhöhte die Abundanz und die Diversität mehrjähriger Kräuter. Allerdings veränderte das unterschiedliche Management nicht die Zusammensetzung von Licht und Schatten liebenden Arten oder weit verbreiteten und Malesianischen Arten.

Die Kräuterdiversität der Wälder Zentralsulawesis war höher als in anderen malesianischen Wäldern. Wir haben zwei Lokalitäten untersucht, eine auf 1000 und die andere auf 1400 m. Auf 1000 haben wir 91 angiosperme Kräuter aus 28 Familien und 112 Farne und Lycophyten aus 15 Familien festgestellt (203 Arten insgesamt). Auf 1400 m fanden wir 77 angiosperme Kräuter aus 25 Familien und 94 Farne und Lycophyten aus 20 Familien (171 Arten insgesamt).

Zusätzlich haben wir ein Höhentransekt von 250 bis 2450 m untersucht und die Artenzahlen zu Umweltfaktoren, wie der Höhe, der Fläche, dem Niederschlag und der Temperatur in Beziehung gesetzt. In dieser Studie fanden wir 302 terrestrische Krautarten aus 51 Familien. Bei der Analyse der Gesamtdiversität fiel auf, dass wir nur eine Beziehung zur Fläche der einzelnen

Höhenstufen Sulawesis nachweisen konnten. Die einzelnen häufig vorkommenden Familien hingegen zeigten signifikante Beziehungen zu verschiedenen Umweltfaktoren. Diese Beziehungen waren allerdings teils negativ und teils positiv und ergaben daher kein einheitliches Muster auf Grundlage der drei Großgruppen Monokotyle, Diekotyle und Farne. Dies spiegelt sich ebenfalls in der Gesamtdiversität wieder. Das generelle Muster der altitudinalen Pflanzendiversität, welches sich aus den Mustern der einzelnen Gruppen zusammensetzt, wurde auch schon in anderen Studien gefunden und scheint ein häufiges Muster in tropischen Bergwäldern zu sein.

Am Ende vergleichen wir Diversitätsmuster von Kräutern in Afrika, Amerika und Asien. Deren Diversität haben wir mit sechs Umweltfaktoren, Höhe, Evopotanspiration (AET), mittlere Durchschnittstemperatur, Minimumtemperatur des kältesten Monats, mittlerer Jahresniederschlag und niederschlag des trockensten Monats in Beziehung gesetzt. Die Artenzahl zeigte einen positiven Zusammenhang mit der Höhe und negativ mit Evopotanspiration (AET), der mittleren Durchschnittstemperatur und der Minimumtemperatur des kältesten Monats. Der interkontinentale Vergleich ergab, dass Farne mit geringerer Artenzahl in den amerikanischen als in den afrikanischen und asiatischen Untersuchungsflächen vorkam. Monokotyle waren häufiger in Afrika als in Asien und Dikotyle seltener in Afrika verglichen mit Asien und Amerika. Auf den unterschiedlichen Kontinenten wurde die Diversität der drei Gruppen von unterschiedlichen Umweltfaktoren bestimmt. Weiterhin besitzt jeder Kontinent einen eigenen Satz von Familien. Wir postulieren daher, dass die Artenzahl innerhalb der Familien gesättigt ist, so dass die höchst mögliche Artenzahl, die durch die Verfügbarkeit von Ressourcen oder der Heterogenität der Umwelt bestimmt wird, erreicht ist. Weiterhin ist es möglich, dass die Artenzahl in den einzelnen Untersuchungsgebieten von evolutieven oder historischen Prozessen beschränkt wird.

ACKNOWLEDGMENTS

My thanks go to my supervisor, Michael Kessler. With him I have developed the project, carrying out novel research, and study the herbaceous diversity of tropical ecosystems. Moreover I had the possibility to conduct my field work in Sulawesi, and other Indonesian islands, experiencing a long sojourn in the tropical forest.

My work project was inside the frame of the multidisciplinary project of "Stability of Rain Forest Margin" STORMA. Project developed in collaboration between the University of Göttingen (Germany) and Indonesia Institutions as: Bogor Agricultural University (Bogor, Java), Tadulako University (Palu, Sulawesi), and the Indonesian Institute of Science (LIPI). Field research was conducted inside the Lore Lindu National Park thanks to the permits from the local authorities. Therefore I would like to thank to the project organization in Germany and in Indonesia. I have to thanks my Indonesian counterparts, from the Tadulako University (Palu) Dr. Ramadhanil Pitopang, and from the Bogor Agricultural University (Bogor, Java) Dr. Sri S. Tjitrosoedirdjo, whit who I had a close collaboration and thanks to their suggestion and help I was in the conditions to conclude my work. I have to thanks to the office in Bogor, Dr. Surya Tarigan, which facilitated considerably the administration issues between me and the Indonesia institutions. The project office in Palu (Sulawesi), in particular I thank Wolfram Lorenz, Muhammad Sigit, Adam Malik, for their irreplaceable work. Beside I want to thanks my assistant from the Tadulaku University (Palu), Atok, Sahar and Fierdaus which helped me in the field and processing thousands of herbarium samples. I have to thanks all the drivers, the farmers from who we rented the cacao plantations, which gave to us the possibility to conduct our project; the porters, the cooks, the helpers from several local villages who helped me to conduct the work, relax and enjoy the beauty of the Indonesia tropical forest. People from who I have learned how to stay in the forest, which places to avoid, enjoy the time whit a glass of palm wine and a bowl of white dry rice.

Importantly, I would like to thanks the source of funding for supporting my research, the University of Göttingen, the German Research Science Foundation (DFG), grant SFB-552 STORMA (Stability of Rainforest Margins). The Synthesys grant, NL-TAF 3536, for the support to visiting the Herbarium of Leiden (The Netherland). The University of Zürich.

In conclusion I thank to the people and my friend at the Institute of Systematic Botany, Zürich. The milieu in the institute was dynamic and supportive, from the coffee break, the "field trip presentation" to the more formal meetings. Lastly, but certainly not the least, I thank my family which from Germany to Indonesia supported my work and my passion in botany.

Curriculum Vitae

Personal

Surname:	CICUZZA
Name:	Daniele
Date of birth:	16th November 1975
Nationality:	Italian

Education

Secondary school:	Agronomist Institute, Frosinone (1996)
Undergraduate University:	University of Rome "La Sapienza"
	Degree in Biology (2003)
Postgraduate University:	Bournemouth University (UK) (2004-2005)
	Aberdeen University (UK) (2006)
Ph.D. thesis:	Diversity and assemblage composition of terrestrial herbaceous plants in tropical forest and agroforest
	Göttingen University (2006-2008)
	Zürich University (2008-2010)

Contribution to the chapters:

Chapter one: Conservation value of cacao agroforestry systems for terrestrial herbaceous species in Central Sulawesi, Indonesia

Conceived the ideas:	40% Daniele Cicuzza, 40% Michael Kessler, 20% Yann Clough
Field work:	80% Daniele Cicuzza, 10% Daniela Leitner, 5% Ramadhanil Pitopang, 5% Sri S. Tjitrosoedirdjo
Analysis design:	50% Daniele Cicuzza, 50% Michael Kessler
Data analysis:	100% Daniele Cicuzza
Writing:	50% Daniele Cicuzza, 50% Michael Kessler

Chapter two: Responses of terrestrial herb assemblages to weeding and fertilization in cacao agroforests in Indonesia

Conceived the ideas:	40% Daniele Cicuzza, 40% Michael Kessler, 20% Yann Clough
Field work:	90% Daniele Cicuzza, 10% Sri S. Tjitrosoedirdjo
Analysis design:	50% Daniele Cicuzza, 50% Michael Kessler
Data analysis:	100% Daniele Cicuzza
Writing:	50% Daniele Cicuzza, 50% Michael Kessler

Chapter three: Terrestrial herb communities of tropical submontane and tropical montane forests in Central Sulawesi, Indonesia

Conceived the ideas:	40% Daniele Cicuzza, 40% Michael Kessler, 7% Ramadhanil Pitopang, 7% Sri S. Tjitrosoedirdjo, 7% S. Robbert Gradstein

Field work:	100% Daniele Cicuzza
Data analysis:	100% Daniele Cicuzza
Writing:	50% Daniele Cicuzza, 50% Michael Kessler

Chapter four: Elevational diversity of terrestrial rainforest herbs: When the whole is less than the sum of its parts

Conceived the ideas:	40% Daniele Cicuzza, 40% Michael Kessler, 20% Sandra Willinghöfer
Field work:	50% Daniele Cicuzza, 50% Sandra Willinghöfer
Analysis design:	50% Daniele Cicuzza, 50% Michael Kessler
Data analysis:	40% Daniele Cicuzza, 60% Sandra Willinghöfer
Writing:	30% Daniele Cicuzza, 40% Michael Kessler, 30% Sandra Willinghöfer

Chapter five: A transcontinental comparison of the diversity and composition of tropical forest understory herbs

Conceived the ideas:	50% Daniele Cicuzza, 50% Michael Kessler
Field work:	40% Daniele Cicuzza, 5% Thorsten Krömer, 15% Axel Poulsen, 5% Thomas Delhotal, 10% Stefan Abrahamczyk, 5% Henry Martinez Piedra, 15% Michael Kessler
Analysis design:	50% Daniele Cicuzza, 50% Michael Kessler
Data analysis:	100% Daniele Cicuzza
Writing:	40% Daniele Cicuzza, 10% Axel Poulsen, 10% Stefan Abrahamczyk, 40% Michael Kessler